I 72.12/2:89-0010/v.1

OCS Study
MMS 89-0010

Study of the Rocky Intertidal Communities of Central and Northern California: Year II

Volume I of III

MMS
U.S. Department of the Interior
Minerals Management Service
Pacific OCS Region

OCS Study
MMS 89-0010

STUDY OF THE ROCKY INTERTIDAL COMMUNITIES OF CENTRAL AND NORTHERN CALIFORNIA
YEAR II
VOLUME I OF III

Prepared by

Kinnetic Laboratories, Inc.
in Association with
The University of California, Santa Cruz,
Moss Landing Marine Laboratories,
and
TENERA Corporation

This study was funded by the
Pacific Outer Continental Shelf Region
of the Minerals Management Service
U.S. Department of the Interior
Los Angeles, California

Under Contract No. 14-12-0001-30057

KLI-R-88-19
December 1988

Kinnetic Laboratories, Inc.
P.O. Box 1040
Santa Cruz, CA 95061

DISCLAIMER

This report has been reviewed by the Pacific Outer Continental Shelf Region, Minerals Management Service, U.S. Department of the Interior and approved for publication. The opinions, findings, conclusions, or recommendations expressed in the report are those of the authors, and do not necessarily reflect the views of the Minerals Management Service. Mention of trade names or commercial products does not constitute endorsement or recommendation for use. This report has not been edited for conformity with Minerals Management Service editorial standards.

PROJECT ORGANIZATION

Project Technical Officer:

Martin F. Golden, Minerals Management Service (MMS)

Progress Report Personnel:

Report Authors:	Dane D. Hardin, Kinnetic Laboratories, Inc. (KLI), Biologist Michael S. Foster, Moss Landing Marine Laboratories (MLML), Ecologist Laurie M. Kiguchi, KLI, Biologist Deborah A. Wilson, KLI, Biologist Andrew P. De Vogelaere, MLML, Biologist (Appendix A - Supplemental Study)
Report Reviewers:	John S. Pearse, UCSC Christopher Harrold, Monterey Bay Aquarium (MBA) Joseph Connell, Peer Review Committee David Phillips, Peer Review Committee Marshall Sylvan, UCSC

Key Project Personnel:

Project Manager:	Alan B. Thum, KLI
Assistant Project Managers:	Dane D. Hardin, KLI Christopher Harrold, MBA
Project Scientists:	John S. Pearse, UCSC Michael S. Foster, MLML Laurie M. Kiguchi, KLI Deborah A. Wilson, KLI
Peer Review Committee:	Joseph Connell, Consultant David Phillips, Consultant
Data Analysis Consultant:	Marshall Sylvan, UCSC
Computer Data Analysts:	Peter Wilde, KLI Jamie Wylde, KLI Keith Kutchins, KLI

PROJECT ORGANIZATION (Continued)

Field Survey Team:

Jay Carroll, TENERA Corp. (TENERA)
Chet Chaffee, UCSC
Andrew De Vogelaere, MLML
Peter Fong, UCSC
Michael Foster, MLML
Dane Hardin, KLI
Christopher Harrold, MBA
Laurie Kiguchi, KLI
Scott Kimura, TENERA
Ken Kronschnabl, KLI
Kathy Langan, KLI
Sue Lisin, KLI
Eric Nigg, MLML
John Pearse, UCSC
Jennifer Pelkan, KLI
Deborah Wilson, KLI

Assistance to KLI in Accessing Field Survey Sites:

Leroy Brock, Pt. Reyes National Seashore
Harlan Brown, Hearst Corporation
A.J. Cooke, Hearst Corporation
John Sansing, Pt. Reyes National Seashore
Mike Mortensen, Sea Ranch Association
TENERA Corporation, Avila Beach

TABLE OF CONTENTS

VOLUME I: Page

List of Figures v

List of Tables xi

PREFACE xiii

ABSTRACT xv

TECHNICAL SUMMARY xvii

INTRODUCTION I-1

LITERATURE REVIEW AND ANALYSIS I-3

  Objectives I-3

  Status I-3

FIELD SUMMARY YEAR II I-5

  Introduction I-5

  Experimental Design I-5

  Methods I-5

    Field Methods I-5
    Taxonomic Methods and Nomenclature I-8
    Data Management Methods I-9

  Project Status I-9

    Field Work I-9
    Laboratory Analysis I-9
    Data Management I-12

  Sampling and Experimental Results I-12

    1. Do the species composition and abundance of organisms in rocky intertidal communities vary with season? Do they vary with latitude? I-12

      Endocladia/Mastocarpus papillatus Assemblage I-13
        Results I-13
        Summary I-25
      Mytilus Assemblage I-25
        Results I-25
        Summary I-33

TABLE OF CONTENTS (Continued)

Page

2. How long does a disturbed (completely cleared) area take to recover after this disturbance? How is recovery time and pattern of recovery (or lack thereof) affected by assemblage, site, latitude, and time of year of disturbance? I-33

Endocladia/Mastocarpus papillatus Assemblage I-38
- Results I-38
- Spring Clearings I-38
- Fall Clearings I-48
- Summary I-48

Mytilus Assemblage I-58
- Results I-58
- Spring Clearings I-58
- Fall Clearings I-67
- Summary I-67

Effects of Size and Severity of Disturbance: Results of Supplemental Study I-81

Conclusions I-82

PROJECT RECOMMENDATIONS I-87

Objectives I-87

Status I-87

REFERENCES I-89

APPENDIX A: Effects of Size and Severity of Disturbance on the Recovery of a Rocky Intertidal Assemblage I-91

APPENDIX B: Data Analysis Equations I-165

VOLUME II

APPENDIX C: Species Summaries Spring 1985 through Fall 1986 II-1

II

TABLE OF CONTENTS (Continued)

Page

VOLUME III

APPENDIX D: Ranked Species Abundances by Site III-1
APPENDIX E: Two-Way ANOVA Results III-159
APPENDIX F: Bray-Curtis Similarity Indices III-217

LIST OF FIGURES

Figure		Page
I-A	Study Site Showing OCS Planning Areas and Region.	xxiii
I-1	Field Survey Sites.	I-6
I-2	Experimental Design of Field Survey.	I-7
I-3	*Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data For Control Plots (Mean of 3 Plots) - Kibesillah Hill (A).	I-17
I-4	*Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Sea Ranch (B).	I-17
I-5	*Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Bolinas (C).	I-18
I-6	*Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Pescadero Rocks (D).	I-18
I-7	*Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Pt. Sierra Nevada (E).	I-19
I-8	*Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Diablo Canyon (F).	I-19
I-9	*Mytilus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Kibesillah Hill (A).	I-29
I-10	*Mytilus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Sea Ranch (B).	I-29
I-11	*Mytilus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Bolinas (C).	I-30
I-12	*Mytilus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Pescadero Rocks (D).	I-30
I-13	*Mytilus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Pt. Sierra Nevada (E).	I-31
I-14	*Mytilus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Diablo Canyon (F).	I-31

II

LIST OF FIGURES (Continued)

Figure		Page
I-15	*Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Kibesillah Hill (A).	I-41
I-16	*Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Sea Ranch (B).	I-41
I-17	*Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Bolinas (C).	I-42
I-18	*Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Pescadero Rocks (D).	I-42
I-19	*Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Pt. Sierra Nevada (E).	I-43
I-20	*Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Diablo Canyon (F).	I-43
I-21	*Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots through Time - Kibesillah Hill (A).	I-45
I-22	*Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots through Time - Sea Ranch (B).	I-45
I-23	*Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots through Time - Bolinas (C).	I-46
I-24	*Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots through Time - Pescadero Rocks (D).	I-46
I-25	*Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots through Time - Pt. Sierra Nevada (E).	I-47
I-26	*Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots through Time - Diablo Canyon (F).	I-47

LIST OF FIGURES (Continued)

Figure — Page

I-27 *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Kibesillah Hill (A). I-51

I-28 *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Sea Ranch (B). I-51

I-29 *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Bolinas (C). I-52

I-30 *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Pescadero Rocks (D). I-52

I-31 *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Pt. Sierra Nevada (E). I-53

I-32 *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Diablo Canyon (F). I-53

I-33 *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Kibesillah Hill (A). I-55

I-34 *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Sea Ranch (B). I-55

I-35 *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Bolinas (C)6 I-56

I-36 *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Pescadero Rocks (D). I-56

I-37 *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Pt. Sierra Nevada (E). I-57

I-38 *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Diablo Canyon (F). I-57

LIST OF FIGURES (Continued)

Figure		Page
I-39	*Mytilus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Kibesillah Hill (A).	I-63
I-40	*Mytilus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Sea Ranch (B).	I-63
I-41	*Mytilus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Bolinas (C).	I-64
I-42	*Mytilus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Pescadero Rocks (D).	I-64
I-43	*Mytilus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Pt. Sierra Nevada (E).	I-65
I-44	*Mytilus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Diablo Canyon (F).	I-65
I-45	*Mytilus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots - Kibesillah Hill (A).	I-68
I-46	*Mytilus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots - Sea Ranch (B).	I-68
I-47	*Mytilus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots - Bolinas (C).	I-69
I-48	*Mytilus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots - Pescadero Rocks (D).	I-69
I-49	*Mytilus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots - Pt. Sierra Nevada (E).	I-70
I-50	*Mytilus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots - Diablo Canyon (F).	I-70
I-51	*Mytilus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Kibesillah Hill (A).	I-74
I-52	*Mytilus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Sea Ranch (B).	I-74
I-53	*Mytilus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Bolinas (C).	I-75
I-54	*Mytilus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Pescadero Rocks (D).	I-75

LIST OF FIGURES (Continued)

Figure Page

I-55 *Mytilus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Pt. Sierra Nevada (E). I-76

I-56 *Mytilus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Diablo Canyon (F). I-76

I-57 *Mytilus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Kibesillah Hill (A). I-78

I-58 *Mytilus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Sea Ranch (B). I-78

I-59 *Mytilus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Bolinas (C). I-79

I-60 *Mytilus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Pescadero Rocks (D). I-79

I-61 *Mytilus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Pt. Sierra Nevada (E). I-80

I-62 *Mytilus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Diablo Canyon (F). I-80

I-63 *Endocladia/Mastocarpus papillatus* Assemblage: Spatial and Temporal Variation in Percent Recovery of Spring-Cleared Plots (Mean of 3 Plots). I-83

I-64 *Endocladia/Mastocarpus papillatus* Assemblage: Spatial and Temporal Variation in Percent Recovery of Fall-Cleared Plots (Mean of 3 Plots). I-83

I-65 *Mytilus* Assemblage: Spatial and Temporal Variation in Percent Recovery of Spring-Cleared and Plots (Mean of 3 Plots). I-84

I-66 *Mytilus* Assemblage: Spatial and Temporal Variation in Percent Recovery of Fall-Cleared Plots (Mean of 3 Plots). I-84

LIST OF TABLES

Table		Page
I-1	Sampling Schedule for Each Assemblage and Site.	I-10
I-2	Summary of Field Activities Performed during Years I and II of the Field Survey.	I-11
I-3	Taxa Sampled in the *Endocladia/Mastocarpus papillatus* Assemblage Control Plots, Spring 1985 - Fall 1986.	I-14
I-4	*Endocladia/Mastocarpus papillatus* Assemblage: p Values for Abundant Taxa in Control Plots with High Probability of Temporal Variation ($p \leq 0.099$, that there was no Temporal Difference).	I-20
I-5	Abundance (Counts) of the Dominant Motile Species in the *Endocladia/Mastocarpus papillatus* Assemblage Control Plots, Spring 1985 - Fall 1986.	I-24
I-6	Taxa Sampled in the *Mytilus* Assemblage Control Plots, Spring 1985 - Fall 1986.	I-26
I-7	Abundance (Counts) of the Dominant Motile Species in the *Mytilus* Assemblage Control Plots, Spring 1985 - Fall 1986.	I-32
I-8	*Mytilus* Assemblage: p Values for Abundant Taxa in Control Plots with High Probability of Temporal Variation ($p \leq .099$, that there was no Temporal Difference).	I-34
I-9	Taxa Sampled in the *Endocladia/Mastocarpus papillatus* Assemblage Spring-Cleared Plots, Summer 1985 - Fall 1986.	I-39
I-10	Abundance (Counts) of the Dominant Motile Species in the *Endocladia/Mastocarpus papillatus* Assemblage Spring-Cleared Plots, Summer 1985 - Fall 1986.	I-44
I-11	Taxa Sampled in the *Endocladia/Mastocarpus papillatus* Assemblage Fall-Cleared Plots, Winter 1986 - Fall 1986.	I-49
I-12	Abundance (Counts) of the Dominant Motile Species in the *Endocladia/Mastocarpus papillatus* Assemblage Fall-Cleared Plots, Winter 1986 - Fall 1986.	I-54
I-13	Taxa Sampled in the *Mytilus* Assemblage Spring-Cleared Plots, Summer 1985 - Fall 1986.	I-59
I-14	Abundance (Counts) of the Dominant Motile Species in the *Mytilus* Assemblage Spring-Cleared Plots, Summer 1985 - Fall 1986.	I-66

LIST OF TABLES (Continued)

Table | Page

I-15 Taxa Sampled in the *Mytilus* Assemblage Fall-Cleared Plots, Winter 1986 - Fall 1986. I-71

I-16 Abundance (Counts) of the Dominant Motile Species in the *Mytilus* Assemblage Fall-Cleared Plots, Winter 1986 - Fall 1986. I-77

Tl

PREFACE

This progress report describes the background and status of activities on Contract No. 14-12-0001-30057 from the Minerals Management Service (MMS), U.S. Department of the Interior to Kinnetic Laboratories, Incorporated (KLI) between 1 October 1985 and 31 December 1986. Discussed are the Literature Review and Analysis, the Year II Field Survey, Laboratory Analysis, Data Management, Data Analysis and Synthesis, and Project Recommendations.

The status of a modification to the original scope of work for studies by a graduate student at Moss Landing Marine Laboratories is also reported (Appendix A). The supplemental study focuses on the effects of size and severity of disturbance on the patterns and rates of recovery from disturbance.

ABSTRACT

Progress is reported for Field Survey Year II (1 October 1985 to 31 December 1986) of a six-year study of central and northern California rocky intertidal communities. Focusing on the area from Pt. Conception to the California-Oregon border, the study objectives are to describe seasonal and successional variation in rocky intertidal community structure; determine the response of rocky intertidal communities to natural and human-induced disturbances and correlate this with successional, seasonal, and latitudinal variation; and correlate life history information and oil toxicity data with data from this and other relevant studies.

Tasks discussed in this report include a Literature Review and Analysis, the Field Survey and associated data work-up, project recommendations, and a supplemental study investigating the effects of plot size and degree of clearing on recovery patterns.

Results are presented for the second year of the Field Survey, a five-year experimental study investigating successional, seasonal, and latitudinal variation and patterns of recovery from disturbance. The study encompasses six sites along the California coast and two biological assemblages, the *Mytilus* assemblage and the *Endocladia/Mastocarpus papillatus* assemblage, at each site. Experimental treatments performed at each site in each assemblage include clearing three plots in spring 1985 and three plots in fall 1985.

Species composition and abundance of the control plots in both assemblages have remained very stable. Some species did have significant seasonal changes in abundance, with generally increased abundances in the fall. There were only slight differences between years (1985 vs. 1986) in the number of species showing significant yearly variation.

Recovery varied among sites and times of clearing. In the *Endocladia/Mastocarpus papillatus* assemblage, all the spring-cleared plots at one site and one or two of the spring-cleared plots at two sites recovered after 18 months. For the fall-cleared plots, recovery occurred only at one site, where all three plots recovered. None of the spring- or fall-cleared plots in the *Mytilus* assemblage have recovered, and the similarity of all disturbed plots relative to the controls remains very low at five sites. The lack of recovery in the *Mytilus* assemblage appears due primarily to the lack of mussel recruitment; mussels are abundant in the control plots but rare in the recovery plots at all sites.

For almost all control and recovery variables measured, the effects of processes or factors associated with sites appear to be more important than those associated with season or latitude.

The supplemental study of the effect of size and severity of disturbance on recovery in the mussel assemblage at one site (Pescadero Rocks) showed that partially cleared plots recover much more quickly than completely cleared plots. When edge effects were removed, there were very few differences related to clearing size.

ACCESS NUMBER 30057.4

STUDY TITLE: Successional and Seasonal Variation of Central and Northern California Rocky Intertidal Communities as Related to Natural and Human-Induced Disturbances.

REPORT TITLE: Study of the Rocky Intertidal Communities of Central and Northern California, Year II, Volumes I, II, and III.

CONTRACT NUMBER(S): MMS 14-12-0001-30057.

SPONSORING OCS REGION: Pacific.

APPLICABLE PLANNING AREA(S): All Planning Areas, All Regions.

FISCAL YEAR(S) OF PROJECT FUNDING: 1983, 1984, 1988, 1990.

COMPLETION DATE OF REPORT: December 1988.

COST(S): FY1983: $755,000; FY1984: $640,000; FY1988: $100,000; FY1990: $117,995; CUMULATIVE PROJECT COST: $1,612,995.

PROJECT MANAGER(S): A.B. Thum.

AFFILIATION: Kinnetic Laboratories, Inc.

ADDRESS: Kinnetic Laboratories, Inc., P.O. Box 1040, Santa Cruz, CA 95061.

PRINCIPAL INVESTIGATOR(S)*: D. Hardin, M.S. Foster, J.S. Pearse, C. Harrold, A.B. Thum.

KEY WORDS: Central and northern California; biology; rocky intertidal; succession; latitude; disturbance; algae; mussels; Mytilus; Endocladia.

BACKGROUND: The susceptibility of the central and northern California coast to impacts from an offshore oil spill pointed to the need to identify areas that would be particularly sensitive to such spills. To this end the MMS developed a two-phase plan to study the intertidal communities of central and northern California. The first phase of this effort was titled "Central and Northern California Coastal Marine Habitats: Oil Residence and Biological Sensitivity Indices." That study provided descriptive information (maps, slides, video tapes, literature review and narrative) of the California coastal intertidal zone north of Point Conception. The present study represents the second phase of the MMS plan and includes a literature review and experimental field studies.

OBJECTIVES: The study objectives are to describe seasonal and successional variation in rocky intertidal community structure; determine the response of rocky intertidal communities to natural and human-induced disturbances and correlate these responses with successional, seasonal, and latitudinal variation; and correlate life history information and oil toxicity data with data from this and other relevant studies.

ACCESS NUMBER 30057.4

DESCRIPTION: This six-year (1983-1989) study is currently in its sixth year. Progress during the third year of the study (1 October 1985 through 31 December 1986) is discussed in this report. Kinnetic Laboratories, Inc. leads the study team, which includes the University of California, Santa Cruz, Moss Landing Marine Laboratories, Monterey Bay Aquarium, and TENERA Corporation.

Focusing on the area from Pt. Conception north to the California-Oregon border, the study utilizes existing literature and a five-year experimental field study to address several ecological questions. The Field Survey encompasses six sites along the California coast and two biological assemblages at each site: the *Mytilus* assemblage and the *Endocladia*/*Mastocarpus papillatus* assemblage. In each assemblage, experimental treatments include clearing plots in spring 1985 and in fall 1985. Quantitative sampling was performed at the time of clearing, three months following each clearing date, and semi-annually thereafter.

A supplemental study investigating the effects of plot size and degree of disturbance on recovery patterns of a rocky intertidal assemblage at one of the Field Survey sites is also being performed (Appendix A to the report). A separate Technical Summary was prepared for this supplemental study.

SIGNIFICANT CONCLUSIONS: Natural variation in control plots in both the *Endocladia*/*Mastocarpus papillatus* and *Mytilus* assemblages showed little temporal variation and demonstrated no latitudinal trends among sites during the two years of study. Seasonal and yearly changes in the species composition and abundance of the *Mytilus* assemblage were generally less than those in the *Endocladia*/*Mastocarpus papillatus* assemblage.

Recovery rates in the *Endocladia*/*Mastocarpus papillatus* assemblage varied between seasons of clearing and show no relationship with latitude. All of the spring-cleared plots at one site and one or two of the spring-cleared plots at two sites have recovered. The fall-cleared plots recovered completely at only one site.

None of the spring or fall clearings in the *Mytilus* assemblage have recovered and similarity of clearings to controls at all sites were low. Recovery rates of fall-cleared plots tended to decline with latitude and may be confounded with differences in mussel abundance with latitude.

Results of the supplemental study indicated that the size of a clearing does not affect succession if the effects of the edges are removed. Results also showed that there are highly significant differences in species composition and recovery rate between completely and partially cleared plots.

STUDY RESULTS: This report describes progress on tasks performed during the report period, including the Literature Review and Analysis task, tasks associated with the Field Survey, and project recommendations. Results of the Field Survey are presented.

Results from the first two years of the Field Survey indicated control plots in the *Endocladia*/*Mastocarpus papillatus* assemblage have undergone few significant temporal changes and changes that have occurred did not show any latitudinal trends.

After 18 months, the spring-cleared plots in the Endocladia/Mastocarpus papillatus assemblage completely recovered at one site and partially recovered (one or two of three plots) at two sites. The similarities of cleared plots to control plots continually increased at most sites. The fall-cleared plots in the Endocladia/Mastocarpus papillatus assemblage completely recovered at only one site after 12 months. Like the spring clearings, most of the fall clearings have continually increased in similarity to the controls. The similarity in the shapes of the spring-cleared and fall-cleared recovery curves within sites suggests that site-specific processes may have a greater effect on succession in this assemblage than do time of disturbance or latitude.

In the Mytilus assemblage, none of the spring clearings have completely recovered, and recovery of all sites has been much slower than the recovery of the spring clearings in the Endocladia/Mastocarpus papillatus assemblage. The similarity of fall-cleared plots to controls in the Mytilus assemblage was very low at all sites. This lack of recovery appears to be primarily attributable to the lack of mussel recruitment. Both spring and fall Mytilus recovery curves had similar shapes within sites, suggesting that site-specific processes have a greater effect on recovery than does time of disturbance.

Results of the supplemental study examining the effects of different degrees of disturbance and patch size on succession in the mussel assemblage at a single site are presented in the Appendix A of the report. Successional patterns depended on the severity of disturbance. Patch size did not affect species abundances when edge effects were removed. Edge effects varied among algal species.

STUDY PRODUCT(S):

Kinnetic Laboratories, Inc. 1988. Study of the rocky intertidal communities of central and northern California, Year II, Volume I, II, III. Prepared in association with the University of California, Santa Cruz, Moss Landing Marine Laboratories, and TENERA Corporation for the Pacific OCS Region, Minerals Management Service, U.S. Dept. of the Interior. Contract No. 14-12-0001-30057. OCS Study, MMS 89-0010.

This project has resulted in the publication of several scientific journal articles and reports. The citations for these publications are included in the References for the Final Report listed above.

*Principal Investigator's affiliation may be different than that listed for Project Manager(s).

I

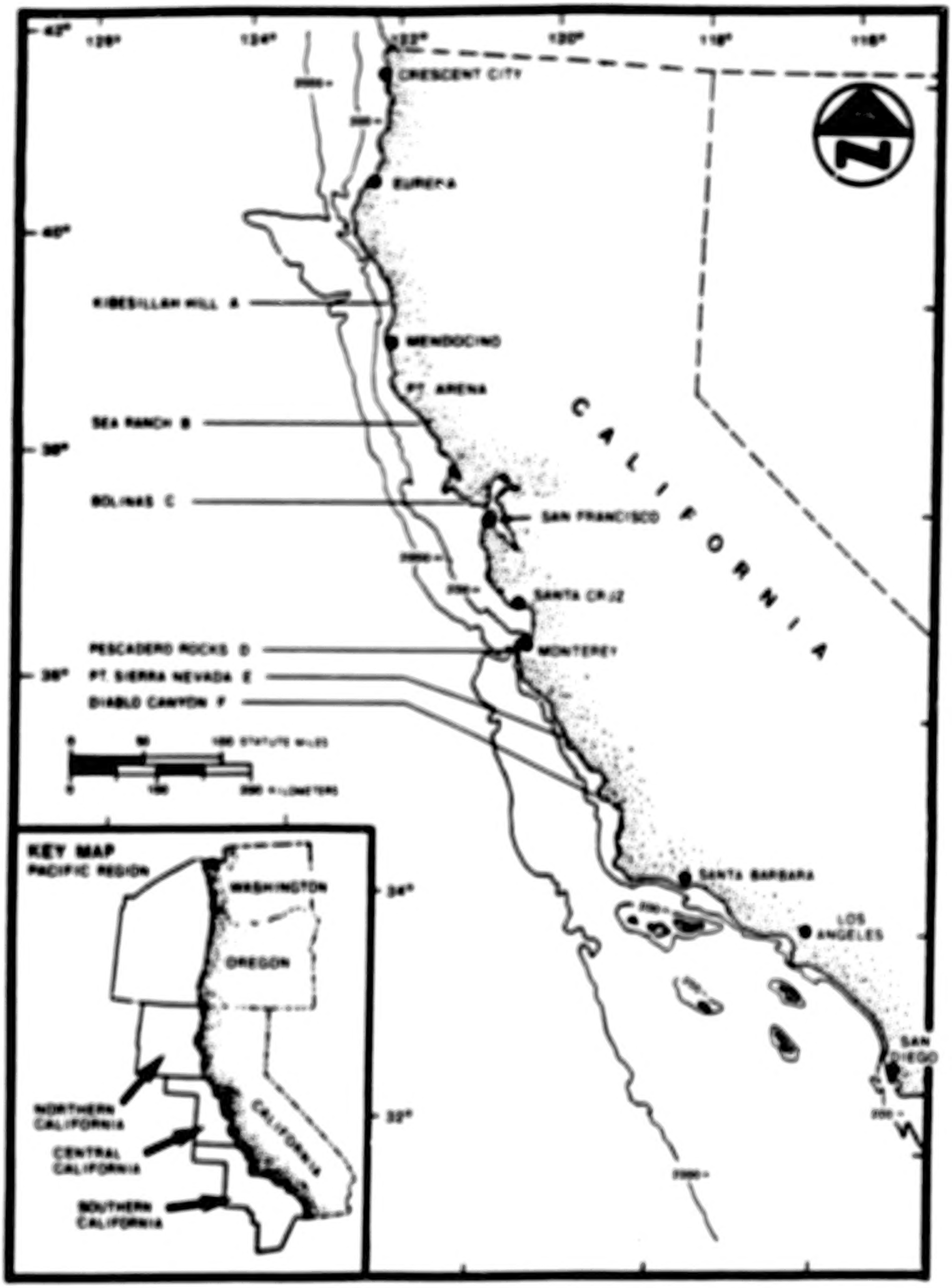


Figure I-A. Study Site Showing OCS Planning Areas and Region.

INTRODUCTION

The objectives of this study, as stated by the Minerals Management Service (MMS) in Request for Proposal (RFP) 3057, are fivefold:

1. To describe seasonal and successional long-term variation in rocky intertidal community structure.
2. To determine the responses of rocky intertidal communities to natural and human-induced disturbances, and to correlate these responses with successional, seasonal, and latitudinal (between Oregon and Pt. Conception) variation.
3. To correlate life history information and oil toxicity data with field data obtained from the study.
4. To compare field data and conclusions of this work with data and conclusions from other relevant studies, including the BLM's Southern California studies (Science Applications Inc., 1979, and associated work).
5. To provide critical background data for controlled oiling experiments or monitoring programs that may be initiated in the future.

In order to pursue these objectives, we formulated the following questions which could be addressed with straightforward sampling and experiments. The questions are:

1. Do the species composition and abundance of organisms in rocky intertidal communities vary with season? Do they vary with latitude (between Oregon and Pt. Conception)?
2. How long does a disturbed (completely cleared) area take to recover after this disturbance? How is recovery time, and pattern of recovery (or lack thereof), affected by:

   - assemblage in which the disturbance took place?
   - site?
   - latitude?
   - time of year in which disturbance took place?

The MMS provided a Statement of Work listing tasks to be performed over the six-year (1983-1989) project period. This report describes progress on tasks performed during the Field Survey Year II (1 October 1985 - 31 December 1986). We consider each of these tasks separately, briefly discussing the objectives and status of the task in each case.

LITERATURE REVIEW AND ANALYSIS

Objectives

The purpose of the Literature Review and Analysis was to evaluate and synthesize all available literature (published or unpublished) pertaining to successional patterns and mechanisms in rocky intertidal communities between British Columbia and Mexico, and the recovery of these communities from natural and human-induced disturbances. An Annotated Bibliography was to be compiled with our evaluations of all literature related to the objectives of this study. A Literature Review and Analysis report was to be submitted to the MMS and a Literature Review manuscript was to be published in a refereed scientific journal. Finally, the information from the Literature Review and Analysis was to be used to make recommendations to the MMS regarding the field program.

Status

The draft Annotated Bibliography was completed in March 1985. After final review by the MMS, the revised document was submitted in April 1987. The bibliography contains more than 1,100 technical reports, Master's theses, doctoral dissertations, student reports, and publications. Each item was reviewed by the project staff and evaluated in terms of its merit and relevance to this study. Each reference includes a full citation, where the work was done, sampling methodology, author(s)' conclusions, and our evaluation of the work.

The final Literature Review and Analysis report (Foster, De Vogelaere, Harrold, Pearse, and Thum, 1986) was submitted to the MMS in September 1986. It is entitled "Causes of Spatial and Temporal Patterns in Rocky Intertidal Communities of Central and Northern California."

The Literature Review and Analysis manuscript, a condensation of the report, was first submitted to the California Academy of Sciences (CAS) on 16 January 1986 to be considered for publication. Review comments were received, the manuscript revised and resubmitted to the CAS in November 1986. It was accepted for publication in late 1987 and published in 1988 in Memoirs of the California Academy of Sciences (Foster, De Vogelaere, Harrold, Pearse, and Thum, 1988).

FIELD SURVEY YEAR II

Introduction

The objective of the Field Survey is to perform the actual field work (sampling and experimental manipulations) required to address the study questions. The Field Survey design was based on extensive preliminary field work as well as results of the Literature Review and Analysis. As described in detail in the annual report for Year I of this study (Kinnetic Laboratories, Inc., 1986), a 20-Site Preliminary Field Survey was performed to obtain physical and biological data which would enable us to select suitable biological assemblages and sites for long-term study. In addition, a methods comparisons study was conducted to determine whether *in situ* random point contact sampling or photoquadrat sampling was the most appropriate and effective way to estimate percent cover. The Field Survey Plan synthesized the results of these studies along with results of the Literature Review and Analysis and presented the final experimental design.

The experimental design and methods were described in detail in the first annual report for this project (Kinnetic Laboratories, Inc., 1986); they are briefly described below. Next is a summary of project status, followed by sampling and experimental results, and conclusions.

Experimental Design

Two rocky intertidal assemblages at each of six sites between Oregon and Point Conception were chosen for long-term sampling. The assemblages chosen were *Endocladia/Mastocarpus papillatus* and *Mytilus*. The six study sites include (from north to south) Kibesillah Hill (A), Sea Ranch (B), Bolinas (C), Pescadero Rocks (D), Pt. Sierra Nevada (E), and Diablo Canyon (F) (Figure 1-1). These six sites have been coded with letters A - F to identify their latitudinal position relative to the other sites. Two seasons were chosen for time of clearing: spring (March-April) and fall (October-November).

The experimental design includes one set of controls and two experimental treatments (spring-cleared and fall-cleared) (Figure 1-2). In each assemblage at each site, four 1 x 2 m plots are established as controls, with three being sampled in any one sampling period on a rotating basis. Six additional 1 x 2 m plots are established as experimental treatments, with three plots cleared (by scraping and burning) during the spring and three plots cleared during the fall (after initial sampling has been performed). The locations of all 10 plots were randomly assigned within the area of each assemblage. Experimental treatments were then randomly assigned to each plot. Each plot is divided into twelve 25 x 25 cm quadrats with a 25-cm buffer zone around the outside of the plot (Figure 1-2).

Methods

Field Methods. At each sampling period, control and treatment (spring-cleared, fall-cleared) plots are sampled in each assemblage at each site. Three quadrats within each plot are quasi-randomly selected for sampling such that there is no overlap between consecutive sampling periods. Sampling methods include random point contact to estimate percent cover of all organisms; counts of motile echinoderms and molluscs; and abundance rankings of motile polychaetes, nemerteans, and arthropods. All three of these methods

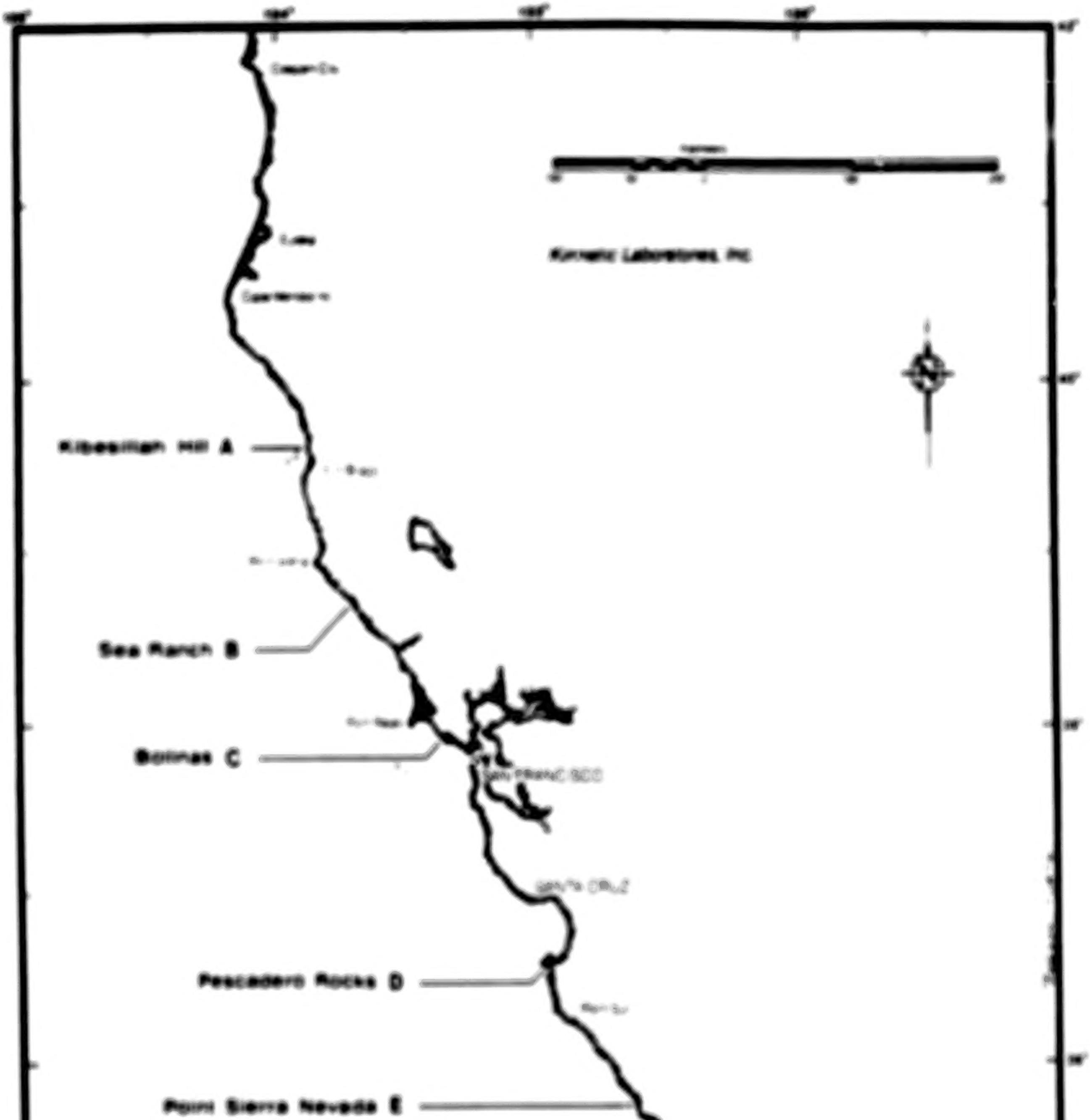


Figure 1-1. Field Survey Sites.

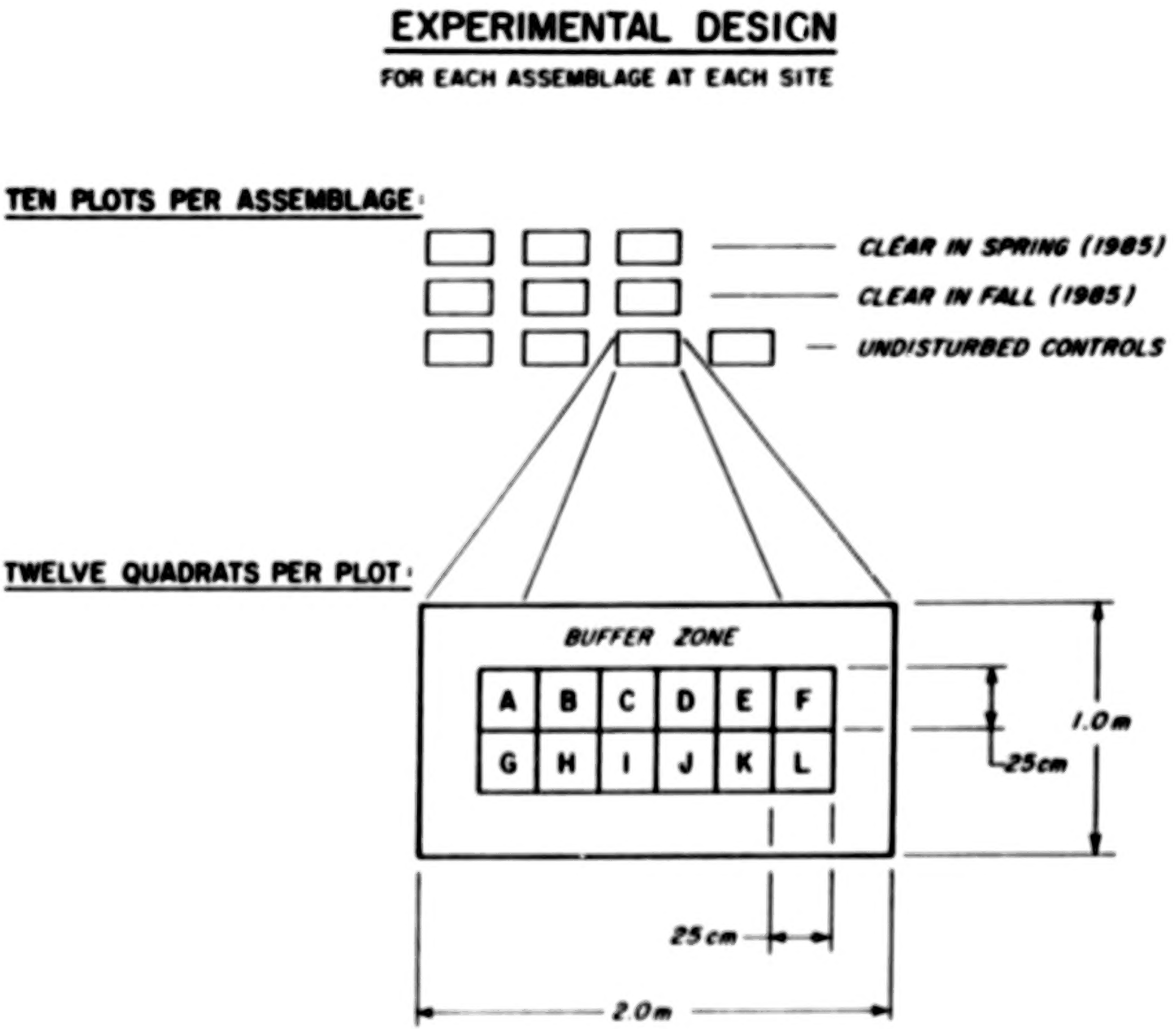


Figure I-2. Experimental Design of Field Survey.

are applied to each of the three replicate quadrats sampled in each plot. The occurrence of more than one species under a point often results in total percent cover exceeding 100.

Clearing of the plots was performed over a three-day period. The process included removal of all organisms using hand tools such as chisels and scrapers, two burning treatments to sterilize the substrate, and brushing with wire brushes. This method of clearing was chosen because it is reproducible and it resulted in a consistent, comparable degree of clearing of all plots at all sites.

Eight photographs are taken of each plot at each sampling period and before and after clearing. Photographs are taken from positions directly above six subareas within each plot, corresponding to the upper left, center, and right; and lower left, center, and right sections of the plot including the surrounding buffer zone. Two oblique photos are taken of the entire plot, one from the bottom and one from the left. A detailed log is kept for all photographs.

Taxonomic Methods and Nomenclature. All algal and invertebrate species are identified to the lowest taxon feasible using Abbott and Hollenberg (1976) or Smith and Carlton (1975). A voucher specimen is collected for each species on a cumulative basis. Specimens are taken from outside the plot or from the buffer zone whenever feasible. Rarely, a specimen is taken from within a plot. The voucher specimens are appropriately preserved and placed in a voucher collection specific to this study. As necessary, species determinations are referred to Dr. I. Abbott (algae), Dr. D. Lindberg (molluscs), or other recognized taxonomic authorities.

When organisms can be identified to genus but not species, the term "sp(p)." is used. The term is used to indicate organisms of either a single unidentified species or several unidentified species. For purposes of this study, *Petrocelis* sp(p). is used to refer both to recognized species of *Petrocelis* and to those that are alternate life stages of the genus *Mastocarpus*. GATGOR is an acronym for "green algae that grow on rocks," commonly seen as a green tinge or slime which cannot be reliably identified to species. GATGOR may comprise a variety of juvenile macrophytes, blue green algae, and diatoms. Some of the difficulty in species identification is due to the lack of key characteristics in the juvenile forms, as well as to the inability to collect voucher specimens without removing the substratum.

To simplify the interpretation of motile species abundance data (counts), individual species of chitons and limpets are combined into "chitons" or "grazer limpets" categories for some analyses. These lumped categories are treated in the analyses as species.

Recent taxonomic revisions have been adopted in this report. Based on morphological, life history and biochemical characteristics, the genus *Mastocarpus* was reinstated for some species of *Gigartina* (Guiry, West, Kim, and Masuda, 1984). *Gigartina papillata* (C. Agardh) J. Agardh 1846 is now referred to as *Mastocarpus papillatus* (C. Agardh) Kutzing 1843 (Guiry *et al.*, 1984). *Gigartina agardhii* Setchell et Gardner 1933, now known as *Mastocarpus jardinii* (J. Agardh) J.A. West comb. nov. 1984 (Guiry *et al.*, 1984), occurs in the study area as well. In addition, *Rhodomela larix* (Turn.) C. Agardh 1822 is now known as *Neorhodomela larix* (Masuda, 1982) and *Odonthalia oregona* Doty 1947 is now known as *Neorhodomela oregona* (Masuda, 1982). All species of the limpet genus *Collisella* Dall 1871 except *Collisella scabra* have been moved to the genus *Lottia* Sowerby 1834 (Lindberg, 1986); quotes are used for *"Collisella" scabra* (Lindberg, 1986).

Eastern Pacific species of the limpet genus *Notoacmaea* Iredale 1915 have been moved to the genus *Tectura* Gray 1847 (Lindberg, 1986).

Data Management Methods. Completed data sheets are first checked by the data base administrator in the field. At the laboratory, counts are totaled for each unique category (e.g., rock, sand, algal or invertebrate species, etc.); counts for unknown specimens are flagged until vouchers have been identified. Each unique category is coded with a pre-determined seven-digit code. Data sheets are checked for accuracy. When vouchers have been identified, their seven-digit codes are entered and data sheets are checked a final time.

Computer raw data files are checked against the data sheets to ensure that each record has been entered correctly. When this has been verified, raw data files are compiled using PRODAS (Conceptual Software, Inc., 1985), a statistical analysis package designed for use on microcomputers. Statistics are generated from the PRODAS files.

Project Status

Field Work. Field efforts during Year II focused on clearing experimental plots in fall 1985, performing follow-up sampling of initial succession in these plots, and performing semi-annual sampling of both spring-cleared and fall-cleared plots and control plots. This corresponds to the sampling schedule proposed in the Field Survey Plan for Year I (Table I-1). In addition, qualitative observations and photographs were taken of the plots at each sampling period, one month after clearing, and between the 1986 spring and fall sampling periods.

The field activity performed during Field Survey Years I and II is summarized in Table I-2. All experimental manipulations have been completed and sampling is now performed on a semi-annual (spring and fall) basis.

Laboratory Analysis. The objective of the laboratory analysis is to preserve, document, and verify or determine the taxonomic identification of species encountered in the field. The laboratory work includes three main components. The first involves sorting, cataloging, and preserving material collected from the disturbed (cleared) quadrats. The second involves cataloging and archiving the photographic slides of the plots. The third involves developing a voucher collection for the verification of species identifications.

Field Survey Year II included clearing experimental plots in fall 1985. Only material scraped from three 25 x 25 cm quadrats (rather than from the entire 1 x 2 m plot) was saved. The material was placed in plastic containers, fixed with buffered formalin in seawater, and taken to KLI. For long-term storage, samples from both spring-cleared and fall-cleared plots were drained of excess liquid, heat-sealed in airtight plastic bags, and placed in watertight containers. Sorting and analyzing this material depends on approval by the MMS.

Laboratory processing of the photographic samples from each sampling period has been performed. The slides of each plot have been catalogued based upon a detailed photographic log which is kept by the photographer. The slides are arranged by station, plot, and time and archived in clear polyethylene pages kept in three-ring binders.

All vouchers from the Year II Field Survey sampling periods have been identified and preserved as appropriate. Voucher specimens collected from the field were fixed in

Table I-1. Sampling Schedule for Each Assemblage and Site.

	1985				1986				1987				1988				1989			
PLOTS	JFM	AMJ	JAS	OND	JFM	AMJ	JAS	OND	JFM	AMJ	JAS	OND	JFM	AMJ	JAS	OND	JFM	AMJ	JAS	OND
Spring-Cleared Plots	C S	S		S	S			S	S			S	S			S	S			
Fall-Cleared Plots				C S	S S			S	S			S	S			S	S			
Control Plots	S	S		S	S S			S	S			S	S			S	S			
	Field Survey Year I				Field Survey Year II															

C = Clear
S = Sample

Table I-2. Summary of Field Activities Performed during Years I and II of the Field Survey (Spring 1985 - Fall 1986).

Activity	Dates
YEAR I	
Marking permanent quadrats	2-7 March 1985
Spring sampling and clearing	17 March - 24 April 1985
Photographs and qualitative notes on spring-cleared plots	6 May - 7 June 1985
Sampling of spring-cleared plots and controls	19 - 24 June 1985
YEAR II	
Fall sampling and clearing	13 October - 16 November 1985
Photographs and qualitative notes on fall-cleared plots	25 November - 17 December 1985
Sampling of fall-cleared plots and controls	6 - 11 January 1986
Semi-annual sampling of all plots	21 - 26 March 1986
Photographs and qualitative observations	21 - 26 September 1986
Semi-annual sampling of all plots	31 October - 14 November 1986

three percent (algae) or 10 percent (invertebrates) buffered formalin in seawater. At the laboratory, algal specimens were removed from formalin and rinsed prior to identification. At least one specimen representing each species found in the study was pressed and dried or preserved in formalin and seawater for inclusion in the voucher collection. Invertebrate vouchers were either dried or transferred to 70 percent ethanol for identification and preservation. Algal specimens are maintained in an herbarium at Moss Landing Marine Laboratories; invertebrate specimens are kept at the KLI laboratory in Santa Cruz. Permanent collection labels and a cumulative cross-reference index have been prepared for all voucher specimens.

Data Management. The objective of the data management program is to provide an orderly, accurate set of data for the analyses required to answer the questions which are being addressed by this study.

The Field Survey Year II encompassed four sampling periods: fall 1985, winter 1986, spring 1986, and fall 1986. Data from all four sampling periods have been taken through the entire data management process.

Sampling and Experimental Results

1. Do the species composition and abundance of organisms in rocky intertidal communities vary with season? Do they vary with latitude?

These questions concern the community characteristics of the natural, uncleared assemblages at the six study sites. In the report on Year I (KLI, 1986) we compared the species composition and abundance, and similarity of the control (uncleared) plots within and between sites at the outset of the study (spring 1985). In addition, seasonal changes between spring and summer 1985 were examined. The data indicated within-site variability in both assemblages, with similarities (Bray-Curtis) among plots ranging from 38 to 83 percent (generally greater than 60 percent). The *Endocladia*/*Mastocarpus papillatus* assemblage was most similar (73 percent) between the two most northern sites [Kibesillah Hill (A) and Sea Ranch (B)]; but similarities among other sites varied between 36 and 58 percent with no clear latitudinal gradient. The among-site comparisons of the *Mytilus* assemblage indicated that the three northern sites [Bolinas (C), Sea Ranch (B), Kibesillah Hill (A)] were more similar to one another than they were to the three southern sites [Diablo Canyon (F), Point Sierra Nevada (E), Pescadero Rocks (D)] and vice versa. Within the *Mytilus* assemblage, the northern sites tended to have a higher cover of mussels; the southern sites had a higher cover of coralline algae. Although there were some seasonal differences at some sites, there were not enough temporal data to determine if these differences were significant, or if there were any latitudinal trends in seasonality.

The results below examine seasonal (spring vs. fall) and annual (1985 vs. 1986) variation in the control plots and whether these variations are correlated with latitude. Data analysis equations are given in Appendix B, abundance data for all taxa found are given in Appendix C, and ranked abundances by site are given in Appendix D. Complete tables for analysis of variance for species with significant probabilities of temporal variation in abundance are provided in Appendix E and Bray-Curtis similarity values are presented in Appendix F.

Our data analysis program computes various community parameters (Shannon diversity, evenness, dominance, etc.) listed at the beginning of Appendix C. Equations used for these parameters are in Appendix B. We have not used these parameters in the Results below because variation in them is not among our current questions. The values are given in Appendix C for those readers who may be interested, and because we may use these data to examine other questions in later reports.

Endocladia/Mastocarpus papillatus Assemblage

Results

The total number of taxa found to date at each site varies between 39 and 73 (Table I-3). There is no apparent trend of either increasing or decreasing taxa richness with latitude. As found in the initial sampling periods (KLI, 1986), Point Sierra Nevada (E) had the lowest number of taxa. Sea Ranch (B) ranked fourth highest in the early sampling periods but is now the richest site.

Percent cover of dominant taxa and unoccupied substrata were plotted against sampling time (Figures I-3 - I-8) to examine overall trends in abundance. Dominant taxa included species characteristic of the assemblage (*Endocladia muricata*, *Mastocarpus papillatus*, and *Balanus glandula*) and/or those with a high cover (>10 percent at any sampling date). Unoccupied substrata included rock (unoccupied substrata with an organism draping over it) and bare rock (unoccupied substrata with no overstory). Taxa are arranged from right (most abundant) to left (least abundant) according to their relative abundance in spring 1985.

With few exceptions, these data give the general impression of little seasonal and year to year change in the abundant taxa; composition of dominant species remained constant and, in most cases, abundances were similar. There is a trend at most sites of decreased abundance of organisms (and increased unoccupied substrata) in the spring relative to fall that is most likely a consequence of winter storms (see review in Foster *et al.*, 1986). Exceptions include the overall increase in *Fucus distichus* at Bolinas (C) (Figure I-5, Table I-4), the overall decline in *Mastocarpus papillatus* at Diablo Canyon (F) since summer 1985 (Figure I-8, Table I-4), and the fall 1986 decline in *Endocladia muricata* at Point Sierra Nevada (E) (Figure I-7).

Limpets and *Littorina scutulata/plena* were the most abundant (density) of the motile taxa that were counted in the plots, but there is considerable within- and between-site variation (Table I-5). The abundances of *L. scutulata/plena* were seasonally variable, particularly at Point Sierra Nevada (E) and Pescadero Rocks (D). *L. scutulata/plena* was most abundant in the fall of 1985 and 1986 at Point Sierra Nevada but most abundant in the summer of 1985 and spring of 1986 at Pescadero Rocks (Table I-5).

Temporal changes in all abundant taxa at each site were analyzed with two-way ANOVAs (season, year; Appendix E). Those taxa that had a high probability of temporal difference in abundance are listed by site in Table I-4. Although there were seasonal trends noted above, relatively few differences in abundances of individual taxa were significant. The number of taxa with significant seasonal differences ranged between zero [Kibesillah Hill (A)] and four [Pescadero Rocks (D)]. The number with significant annual differences ranged between zero [Kibesillah Hill (A)] and three [Diablo Canyon (F), Sea Ranch (B)]. All the apparently large changes noted above in Figures I-3 - I-8 and Table I-5 were significant. Most of the taxa with significant seasonal differences were more

__Table I-3__. Taxa Sampled in the *Endocladia/Mastocarpus papillatus* Assemblage Control Plots Spring 1985 - Fall 1986.

SITE:	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
__SPECIES__						
Acanthina sp(p).			X			X
Amphipods, unident.	X	X	X	X	X	X
Analipus japonicus		X	X	X		
Anthopleura elegantissima	X	X	X			X
Anthopleura xanthogrammica	X	X				
Arachnids, unident.	X					
Articulated corallines (juv.)	X					
Balanus glandula	X	X	X	X	X	
Balanus sp(p).	X					
Barleeia sp(p).			X			
Bittium attenuatum			X			X
Bittium eschrichtii						X
Bossiella orbigniana ssp. *dichotoma*		X				
Bossiella plumosa	X	X		X		
Brown crusts		X				
Ceramium eatonianum		X	X	X		X
Chaetomorpha linum				X	X	
Chthamalus sp(p).	X	X	X	X	X	X
Cirratulids, unident.		X	X			
Cladophora columbiana	X	X	X	X	X	X
"Collisella" scabra	X	X	X	X	X	X
Colpomenia peregrina			X			
Colpomenia sinuosa			X			
Corallina officinalis				X		
Corallina sp(p).				X		
Corallina vancouveriensis	X	X	X	X	X	X
Cottids, unident.		X				
Crustose corallines, unident.	X	X	X	X	X	X
Cryptosiphonia woodii	X	X	X			
Cylindrocarpus rugosus				X		
Decapods, unident.						X
Diatoms, unident.		X			X	
Diptera-Diptera larvae		X		X	X	X
Endocladia muricata	X	X	X	X	X	X
Epitonium tinctum	X	X	X			X
Fucus distichus	X	X	X			X
G.A.T.G.O.R.	X	X		X	X	X
Gelidium coulteri	X		X	X		X
Gelidium coulteri/G. pusillum (juv.)						X
Gelidium pusillum			X	X		X
Gigartina canaliculata					X	X
Gigartina leptorhynchos						X
Grapsids, unident.				X		

Table I-3. Continued.

SITE:	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
SPECIES						
Green blades	X		X			
Haliclona permollis						X
Haliotis cracherodii						X
Halosaccion glandiforme	X	X				
Hemigrapsus nudus		X		X		X
Hesperophycus harveyanus					X	X
Insects, unident.				X		X
Iridaea flaccida	X	X	X	X		X
Iridaea heterocarpa	X	X		X		X
Isopods, unident.	X	X	X			
Lacuna sp(p).	X	X				
Lasaea subviridis				X		
Lepidochitona dentiens	X	X	X	X	X	X
Lepidochitona hartwegii				X	X	X
Leptasterias sp(p).		X				
Littorina keenae	X					X
Littorina scutulata/plena	X	X	X	X	X	X
Littorina sp(p).				X		X
Lottia asmi	X	X	X	X		X
Lottia digitalis	X	X	X	X	X	X
Lottia gigantea		X		X		
Lottia limatula		X	X	X	X	X
Lottia paradigitalis	X	X	X	X	X	X
Lottia pelta	X	X	X	X	X	X
Lottia sp(p).	X	X	X	X	X	X
Mastocarpus jardinii		X		X		
Mastocarpus papillatus	X	X	X	X	X	X
Microcladia borealis		X				
Mitrella carinata					X	
Mopalia muscosa			X		X	X
Mytilus californianus	X	X	X	X	X	
Nemerteans, unident.	X	X		X	X	X
Neorhodomela larix	X	X				
Neorhodomela oregona	X					
Nereids, unident.		X				
Nucella emarginata	X	X	X	X	X	X
Nuttallina californica		X		X	X	X
Ocenebra circumtexta						X
Ocenebra interfossa			X			X
Odonthalia floccosa	X	X	X			
Pachygrapsus crassipes	X	X	X	X	X	X
Pagurus sp(p).	X	X	X	X	X	X
Pelvetia-Pelvetiopsis sp(p).	X	X	X	X	X	X
Petrocelis sp(p).	X	X	X	X	X	X

Table I-3. Continued.

SITE:	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
SPECIES						
Petrolisthes cinctipes	X	X				X
Phaeostrophion irregulare			X			
Phragmatopoma californica		X				X
Phyllospadix scouleri	X					
Pollicipes polymerus				X		
Polychaetes, unident.	X	X		X		X
Poriferans, unident.		X				
Porphyra lanceolata		X				X
Porphyra perforata	X	X	X	X	X	X
Porphyra sp(p).	X	X				
Prionitis lanceolata		X				
Pterocladia caloglossoides	X					
Pterocladia capillacea			X			
Pterosiphonia pennata			X			
Pycnogonids, unident.		X				
Ralfsia sp(p).	X	X	X			X
Red crusts	X	X	X	X	X	X
Rhodoglossum affine				X		X
Searlesia dira		X			X	
Semibalanus cariosus	X	X	X			
Septifer bifurcatus		X				
Sipunculids, unident.		X				
Spirorbids, unident.						X
Tectura scutum		X				X
Tegula brunnea		X				
Tegula funebralis	X	X	X	X	X	X
Tonicella lineata		X				
Ulva californica				X	X	
Ulva lobata				X	X	
Ulva sp(p).		X		X	X	
TOTAL TAXA	53	73	51	56	39	63

DC = Diablo Canyon, PSN = *Pt.* Sierra Nevada, PR = Pescadero Rocks, B = Bolinas, SR = Sea Ranch, KH = Kibesillah Hill; (A-F) designate latitudinal order (A = most northern, F = most southern site).

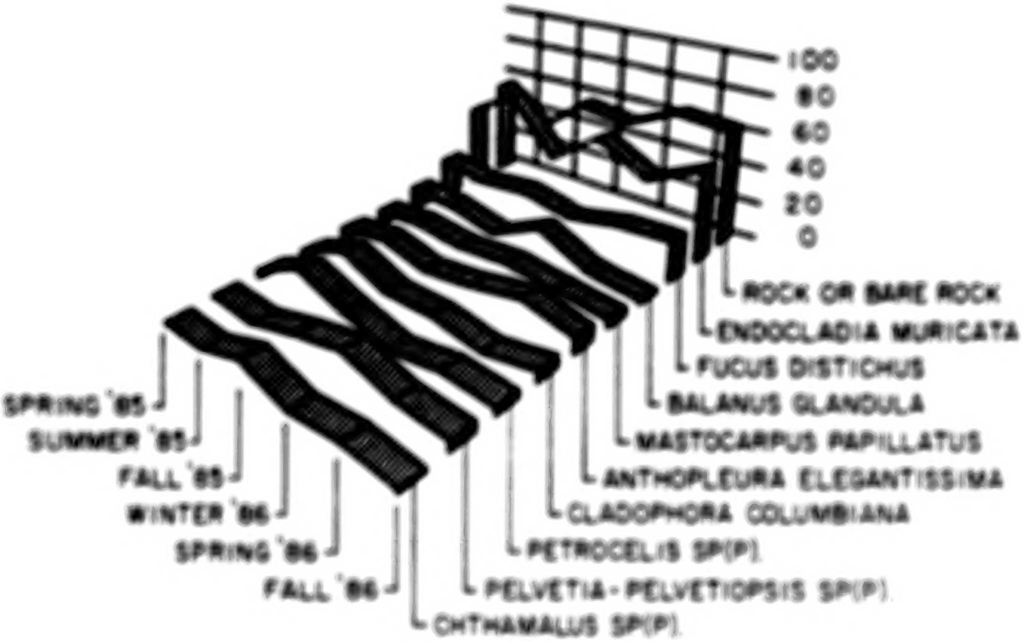


Figure 1-3. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data For Control Plots (Mean of 3 Plots) - Kibesillah Hill (A).

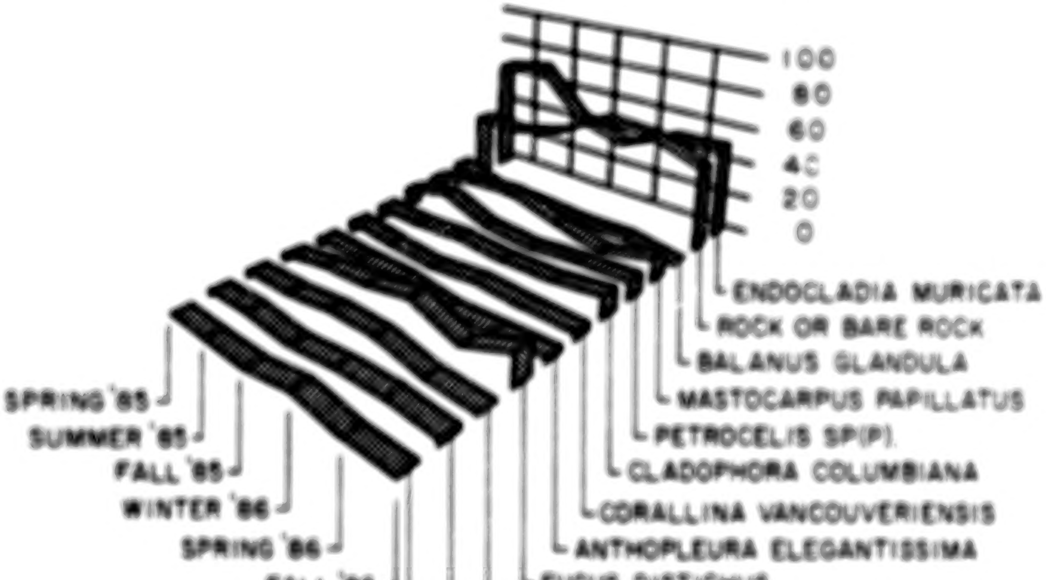


Figure 1-4. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Sea Ranch (B).

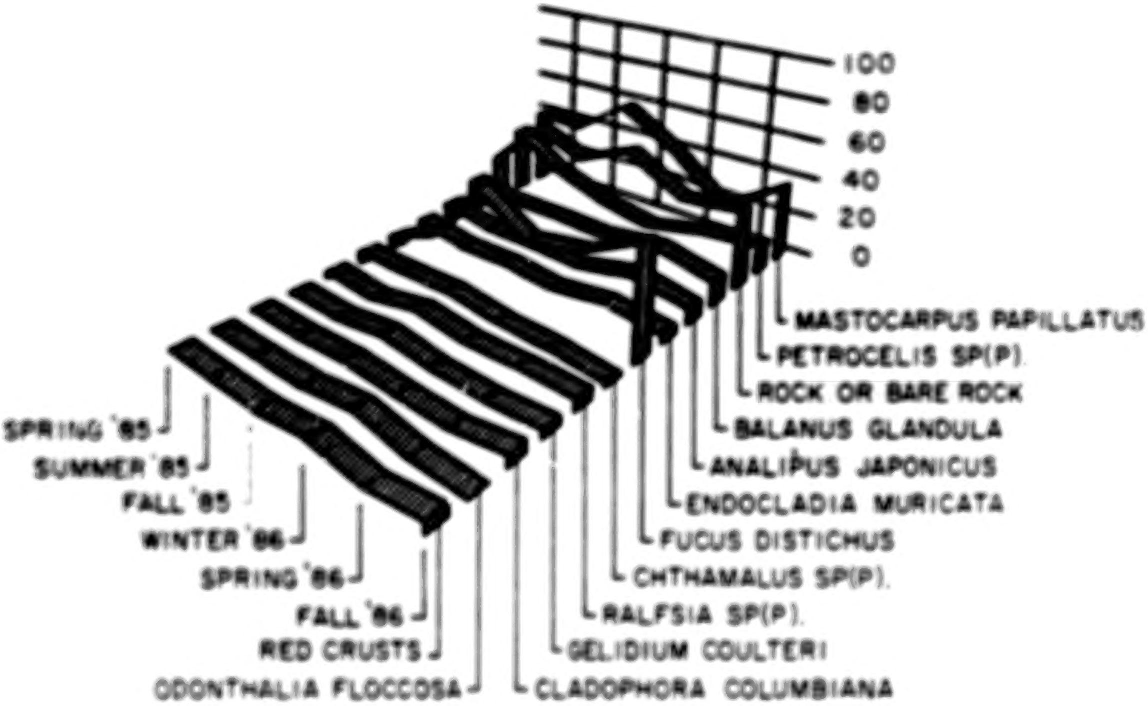


Figure 1-5. *Endocladia/Mastocarpus papillata* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Bolinas (C).

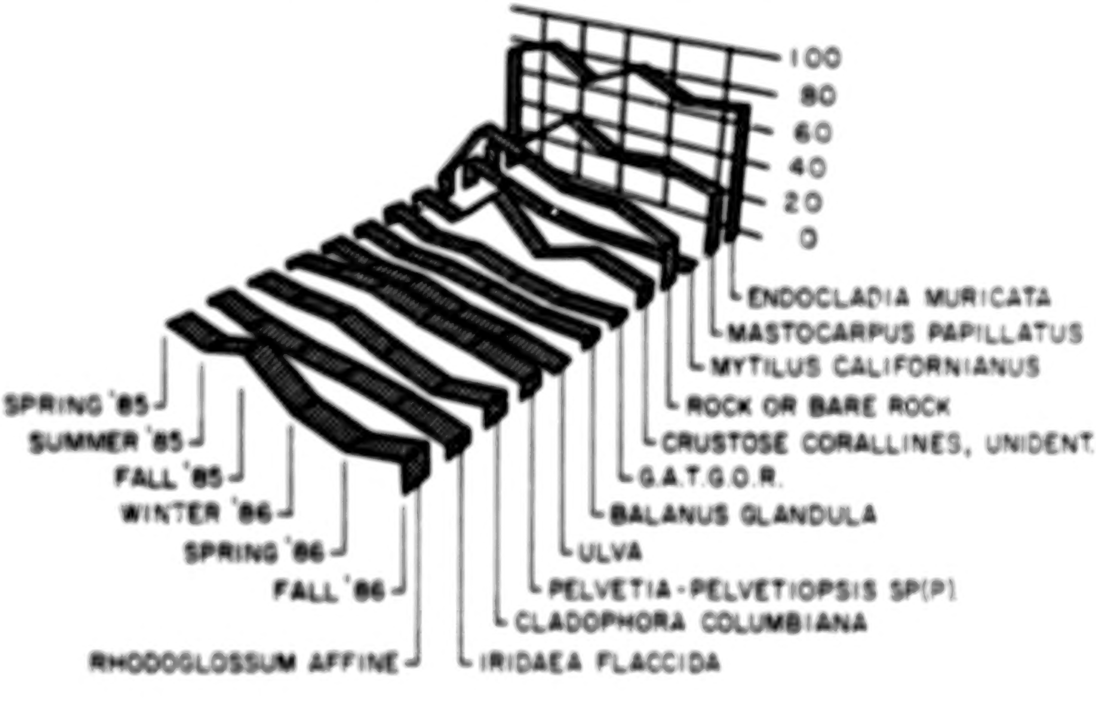


Figure 1-6. *Endocladia/Mastocarpus papillata* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Pescadero Rocks (D).

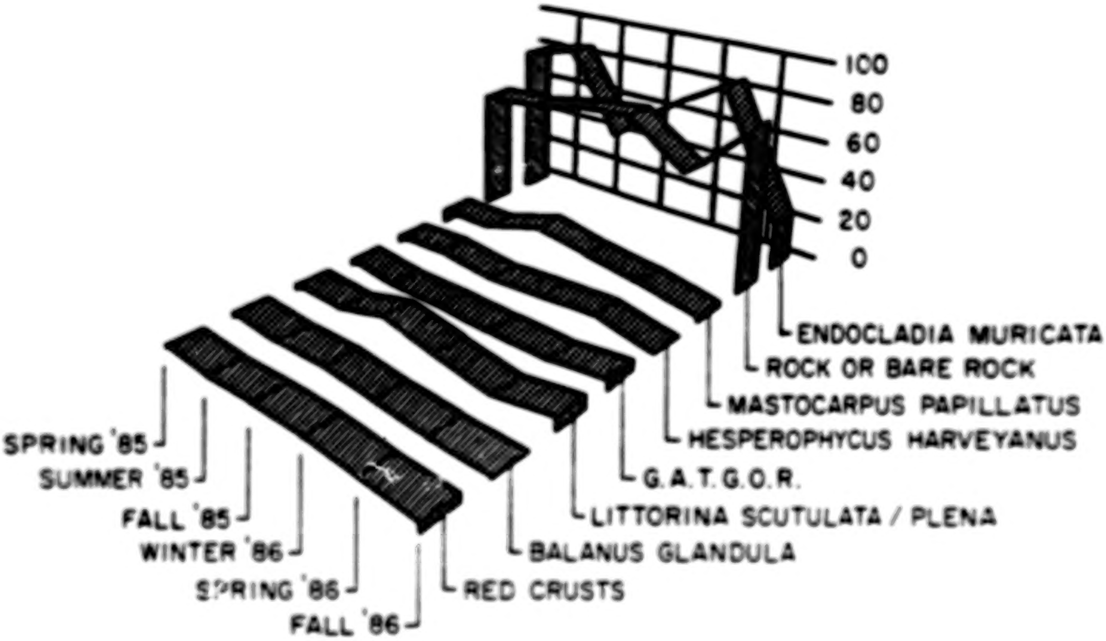


Figure I-7. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Pt. Sierra Nevada (E).

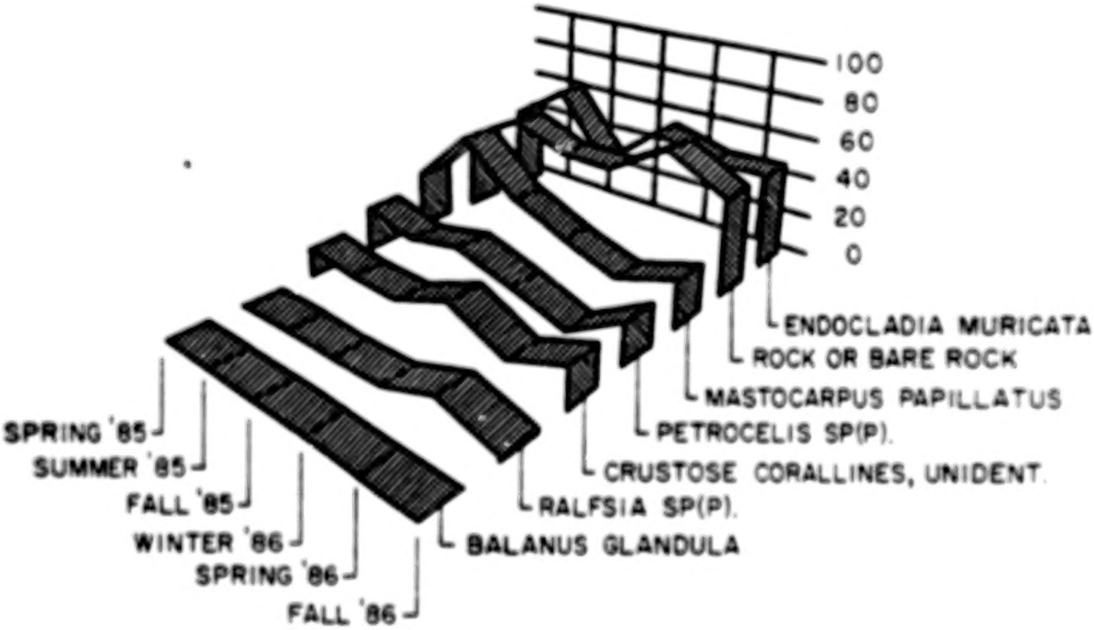


Figure I-8. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Diablo Canyon (F).

Table I-4. ***Endocladia/Mastocarpus papillatus*** **Assemblage: p Values for Abundant Taxa in Control Plots with High Probability of Temporal Variation ($p \leq 0.099$, that there was no Temporal Difference).**

		Temporal Variable[1]		
Site	Species	Season[2]	Year[3]	Y x S[4]
Kibesillah Hill (A)	Sessile:			
	Endocladia muricata			0.02
	Chthamalus sp(p).			0.08
	TOTAL SPECIES	0	0	2
Sea Ranch (B)	Sessile:			
	Chthamalus sp(p).		0.09 (85)	
	Motile:			
	Littorina scutulata/plena		0.09 (86)	
	Nucella emarginata	0.08 (S)	0.03 (86)	
	TOTAL SPECIES	1	3	0
Bolinas (C)	Sessile:			
	Fucus distichus	0.01 (F)	0.05 (86)	0.09
	Mastocarpus papillatus	0.04 (F)	0.02 (85)	
	Petrocelis sp(p).	0.09 (S)		0.04
	TOTAL SPECIES	3	2	2

Table I-4. Continued.

		Temporal Variable		
Site	Species	Season	Year	Y x S
Pescadero Rocks (D)	Sessile:			
	Cladophora columbiana	0.001 (F)		0.08
	GATGOR		0.08 (85)	
	Crustose corallines			0.06
	Rhodoglossum affine	0.01 (F)		
	Mytilus californianus	0.09 (F)	0.07 (85)	
	Motile:			
	Littorina scutulata/plena	0.08 (S)		
	TOTAL SPECIES	4	2	2
Point Sierra Nevada (E)	Sessile:			
	Hesperophycus harveyanus	0.08 (S)[a]		
	Endocladia muricata	0.001 (S)		
	Mastocarpus papillatus			0.05
	Balanus glandula	0.08 (85)		
	Motile:			
	Littorina scutulata/plena	0.0004 (F)		
	TOTAL SPECIES	3	1	1

Table I-4. Continued.

		Temporal Variable		
Site	**Species**	**Season**	**Year**	**Y x S**
Diablo Canyon (F)	**Sessile:**			
	Ralfsia sp(p).		0.03 (86)[6]	
	Mastocarpus papillatus		0.05 (85)[7]	
	Petrocelis sp(p).	0.03 (F)[8]	0.02 (85)	0.03
	Motile:			
	Grazer Limpets	0.0003 (F)		0.03
	Littorina scutulata/plena			0.04
	Nucella emarginata			0.02
	TOTAL SPECIES	2	3	4

Table I-4. Continued.

SUMMARY

SEASONAL AND YEAR TO YEAR CHANGES VS. LATITUDE

Number of Taxa with High Probability of Difference in Abundance:

	Sites					
	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
Season	0	1	3	4	3	2
Year to Year	0	3	2	2	1	3

---

[1] From ANOVA's in Appendix E. A blank = p > .099

[2] Fall vs. Spring; numbers are p values

[3] 1985 vs. 1986; numbers as in 2.

[4] Year-Season interaction; numbers as in 2.

[5] (S) Spring > Fall

[6] (85) 1985 > 1986

[7] (86) 1986 > 1985

[8] (F) Fall > Spring

Note: Complete ANOVA analyses for all abundant taxa (Sessile: >10% cover at any site at any time; Motile: >15 individuals/m^2 at any site at any time) with significant probabilities are shown in Appendix E.

Table I-5. Abundance (Counts) of the Dominant Motile Species in the *Endocladia/Mastocarpus papillatus* Assemblage Control Plots, Spring 1985 - Fall 1986. Mean* (Standard Deviation).

Sampling Name Period	Kibesillah Hill (A)		Sea Ranch (B)		Bolinas (C)		Pescadero Rocks (D)		Pt. Sierra Nevada (E)		Diablo Canyon (F)	
CHITONS												
Spring 85	0.67	(1.15)	0.00	(0.00)	0.00	(0.00)	3.42	(4.82)	0.67	(1.15)	0.00	(0.00)
Summer 85	0.33	(0.58)	1.00	(1.73)	0.00	(0.00)	0.67	(1.15)	0.00	(0.00)	1.33	(0.58)
Fall 85	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	2.75	(3.19)
Winter 86	0.33	(0.58)	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)	0.00	(0.00)	0.33	(0.58)
Spring 86	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)	2.42	(3.36)	0.00	(0.00)	0.33	(0.58)
Fall 86	0.00	(0.00)	0.67	(1.15)	0.33	(0.58)	4.75	(6.57)	0.00	(0.00)	0.67	(1.15)
GRAZER LIMPETS												
Spring 85	103.50	(73.50)	120.25	(76.28)	33.08	(13.70)	17.33	(24.21)	16.58	(28.72)	3.33	(2.89)
Summer 85	68.50	(25.64)	121.33	(81.94)	71.33	(56.68)	12.92	(8.27)	0.00	(0.00)	12.17	(11.41)
Fall 85	77.50	(50.14)	89.08	(36.17)	43.25	(30.39)	28.08	(4.26)	5.75	(3.19)	55.58	(12.41)
Winter 86	177.25	(126.22)	80.50	(53.95)	12.00	(14.95)	7.67	(4.04)	7.83	(11.84)	14.33	(4.65)
Spring 86	63.33	(36.15)	116.33	(71.19)	51.33	(42.57)	35.42	(28.28)	4.08	(6.23)	15.08	(9.14)
Fall 86	25.42	(25.09)	44.58	(25.07)	78.33	(41.79)	51.67	(17.31)	0.67	(1.15)	35.08	(13.16)
LITTORINA SCUTULATA/PLENA												
Spring 85	249.50	(420.70)	0.00	(0.00)	179.50	(361.97)	108.58	(35.34)	253.42	(41.07)	4.42	(4.16)
Summer 85	97.42	(111.97)	12.42	(13.29)	138.92	(154.78)	686.42	(404.95)	152.42	(30.61)	28.25	(21.87)
Fall 85	333.83	(384.13)	3.67	(3.21)	348.42	(241.22)	4.50	(6.95)	1136.42	(514.19)	41.67	(35.54)
Winter 86	181.58	(275.60)	4.83	(6.71)	165.83	(138.68)	14.58	(25.26)	600.58	(370.01)	3.75	(3.31)
Spring 86	92.83	(80.96)	8.33	(7.22)	189.08	(152.19)	223.25	(212.74)	197.83	(74.16)	19.08	(15.97)
Fall 86	75.92	(36.45)	13.83	(14.55)	108.83	(99.70)	62.50	(81.25)	1037.08	(46.23)	0.33	(0.58)
NUCELLA EMARGINATA												
Spring 85	9.17	(15.02)	0.33	(0.58)	0.33	(0.58)	0.33	(0.58)	0.00	(0.00)	0.33	(0.58)
Summer 85	0.33	(0.58)	3.33	(4.04)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	1.33	(0.58)
Fall 85	2.08	(3.61)	0.00	(0.00)	1.00	(1.73)	0.00	(0.00)	0.00	(0.00)	0.67	(0.58)
Winter 86	3.75	(4.18)	1.00	(1.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	1.67	(1.53)
Spring 86	2.00	(1.00)	2.33	(1.53)	0.67	(0.58)	0.00	(0.00)	0.00	(0.00)	1.33	(0.58)
Fall 86	0.67	(1.15)	0.67	(0.58)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
TEGULA FUNEBRALIS												
Spring 85	23.08	(14.36)	2.00	(1.73)	17.67	(3.79)	0.33	(0.58)	0.33	(0.58)	35.75	(26.96)
Summer 85	31.33	(25.58)	5.00	(6.08)	10.67	(2.08)	0.00	(0.00)	0.33	(0.58)	49.25	(9.09)
Fall 85	14.00	(4.36)	0.00	(0.00)	12.67	(5.51)	0.33	(0.58)	1.00	(1.73)	33.75	(22.45)
Winter 86	15.00	(5.00)	4.00	(6.08)	14.33	(8.96)	0.00	(0.00)	2.67	(2.52)	53.08	(17.90)
Spring 86	39.67	(35.22)	0.33	(0.58)	20.08	(22.66)	0.00	(0.00)	0.00	(0.00)	29.67	(11.85)
Fall 86	10.00	(6.95)	2.67	(4.62)	17.33	(9.71)	0.00	(0.00)	1.00	(1.73)	23.33	(6.81)

*Mean number of individuals per 3 plots [value for each plot based on (sum of counts for 3 quadrats) ÷ 0.1875 sq.m).

abundant in the fall (8 of 13), and most with significant annual differences were more abundant in 1985 (7 of 11).

Based on the number of taxa that had a high probability of temporal difference in abundance, there appear to be no latitudinal trends in either significant seasonal or annual differences (Summary, Table I-5). The two most northern sites had the lowest number of taxa with significant seasonal change, but Diablo Canyon (F) was next lowest and Pescadero Rocks (D) was highest. There are no apparent correlations between latitude and the number of taxa/site with significant annual differences.

Summary

These results indicate that the control plots used to characterize the *Endocladia/Mastocarpus papillatus* assemblage have undergone few significant changes during the two years of study. Moreover, changes that were observed are not apparently related to processes that vary along the latitudinal gradient. This latter conclusion is perhaps best exemplified by individual species such as *Endocladia muricata*, the most abundant organism in this assemblage at five of the six sites. Its abundance varied with season (Figures I-3 - I-8) but significant seasonal variation was detected only at Point Sierra Nevada (E) (Table I-4) and patterns varied with each site. This is surprising as it might be expected that a species would show similar patterns of seasonal variation at most sites even if the amount of variation was unrelated to latitude. It suggests that site-specific processes have the greatest effects on temporal variation in species composition and abundance in this assemblage.

Mytilus Assemblage

Results

The total number of taxa found to date in the control plots at each site varied between 40 and 68 (Table I-6). The low richness at the three northern sites suggests a latitudinal trend or a negative association with high mussel cover (Figures I-9 - I-14). However, the most southerly site, Diablo Canyon (F), also had a low richness and relatively low abundance of mussels (Figure I-14). The greatest number of taxa were found at Point Sierra Nevada (E), a site with over 80 percent mussel cover.

As with the *Endocladia/Mastocarpus papillatus* assemblage, the abundances (cover) of the most dominant taxa and unoccupied substrata were plotted against time to indicate temporal patterns in the assemblage (Figures I-9 - I-14). Mussels and *Balanus glandula* were included in all these graphs because they are generally characteristic of the assemblage. Other species were included if their abundance at a site exceeded 10 percent cover at any sampling date. Rank order (right to left) is based on abundances at the first sampling time.

Species composition has remained similar at each site and, with the exception of barnacles and *Mastocarpus papillatus* at Bolinas (C) (Figure I-11), and *Mytilus californianus* at Pescadero Rocks, Figure I [illegible] overall seasonal and annual changes were slight. Abundance data for motile organisms clearly show that limpets were the most common motile animals sampled, but there are no obvious temporal trends (Table I-7).

Temporal variations for all abundant taxa were analyzed with two-way ANOVAs (season, year; Appendix E), and those taxa with significant differences were listed in Table

Table I-6. Taxa Sampled in the *Mytilus* Assemblage Control Plots, Spring 1985 - Fall 1986.

SPECIES	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
Acanthina sp(p).					X	
Amphipoda, unident.	X	X	X	X	X	X
Amphissa versicolor	X					
Analipus japonicus		X		X	X	X
Anthopleura elegantissima	X	X	X	X	X	X
Anthopleura xanthogrammica						X
Arachnida, unident.	X			X		
Articulated corallines (juv.)				X		
Balanus glandula	X	X	X	X	X	X
Balanus nubilis				X		
Binghamia sp(p).				X		
Bittium attenuatum			X			
Bittium eschrichtii			X			
Bossiella plumosa				X	X	X
Brown crusts				X		
Calliarthron sp(p).						X
Calliarthron tuberculosum				X		
Callithamnion pikeanum		X			X	X
Callithamnion rupicolum						X
Caridea, unident.				X		
Ceramium eatonianum			X			
Chrysophyta, unident.		X		X	X	X
Chthamalus sp(p).	X	X	X	X	X	X
Cirratulidae, unident.					X	
Cirripedia, unident.		X				
Cladophora columbiana				X	X	X
"Collisella" scabra	X	X	X	X	X	X
Corallina officinalis				X		
Corallina sp(p).				X		
Corallina vancouveriensis		X		X	X	X
Crepidula adunca	X					
Crustose corallines, unident.	X	X	X	X	X	X
Cumagloia andersonii				X		
Cyanophyta, unident.		X				
Cylindrocarpus rugosus				X	X	X
Decapoda, unident.			X			
Diptera-Diptera larvae	X	X	X	X		
Egregia menziesii				X	X	
Endocladia muricata	X	X	X	X	X	X
Farlowia conferta					X	
Fissurella volcano				X	X	
Fucus distichus		X				
G.A.T.G.O.R.				X	X	
Gelidium coulteri			X			

Table 1-6. (Continued)

SPECIES	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
Gelidium pusillum			X		X	X
Gigartina canaliculata			X			
Green blades					X	
Halichondria panicea				X	X	
Haliclona permollis				X		
Haliclona sp(p).				X		
Halosaccion glandiforme		X				
Hemigrapsus nudus	X	X	X		X	
Henricia leviuscula				X		
Insecta, unident.	X	X	X			
Iridaea flaccida	X	X		X	X	X
Isopoda, unident.	X	X		X	X	X
Lepidochitona dentiens			X		X	X
Lepidochitona hartwegii				X		X
Leptasterias sp(p).				X	X	
Leptoplanidae, unident.	X	X				
Lindaria succincta	X					
Littorina keenae	X				X	X
Littorina scutulata/plena	X	X	X	X	X	X
Littorina sp(p).						X
Lottia asmi	X	X	X	X	X	X
Lottia digitalis	X	X	X	X	X	X
Lottia gigantea				X		X
Lottia limatula	X	X		X	X	X
Lottia paradigitalis	X	X	X	X	X	X
Lottia pelta	X	X	X	X	X	X
Lottia sp(p).	X	X	X	X	X	X
Mastocarpus papillatus	X	X	X	X	X	
Microcladia borealis					X	
Mopalia lignosa	X					
Mopalia muscosa	X	X				
Mytilus californianus	X	X	X	X	X	X
Mytilus edulis				X		
Mytilus sp(p).			X			
Nemertea, unident.		X		X	X	X
Nereidae, unident.					X	
Nucella emarginata	X	X	X	X	X	X
Nuttallina californica	X	X	X	X	X	X
Pachygrapsus crassipes	X	X	X		X	X
Pagurus sp(p).	X		X		X	
Pelvetia-Pelvetiopsis sp(p).		X		X	X	
Petrocelis sp(p).	X	X	X	X	X	X
Petrolisthes cinctipes			X			
Phragmatopoma californica			X		X	X
Plocamium violaceum					X	

Table I-6. (Continued)

SPECIES	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
Pollicipes polymerus	X	X	X	X	X	X
Polyplacophora, unident.				X		
Polysiphonia hendryi				X	X	X
Polysiphonia nathaniellii					X	
Polysiphonia sp(p).		X			X	
Porifera, unident.				X		
Porphyra lanceolata					X	
Porphyra perforata	X	X	X	X	X	X
Porphyra sp(p).	X	X		X		
Postelsia palmaeformis					X	
Prionitis lanceolata				X		
Pterocladia caloglossoides			X		X	
Ralfsia sp(p).	X	X		X	X	X
Red blades		X		X	X	
Red crusts	X	X	X	X	X	
Rhodoglossum affine					X	
Semibalanus cariosus	X	X		X		X
Sipuncula, unident.		X	X		X	X
Strongylocentrotus purpuratus		X			X	X
Tectura scutum		X	X			
Tegula brunnea	X					
Tegula funebralis	X	X	X		X	
Tetraclita rubescens				X	X	X
Ulva californica				X	X	
Ulva lobata				X	X	
Ulva sp(p).				X	X	
TOTAL TAXA	42	49	41	66	68	47

KH = Kibesillah Hill, SR = Sea Ranch, B = Bolinas, PR = Pescadero Rocks, PSN = Pt. Sierra Nevada, DC* = Diablo Canyon. (A-F) designate latitudinal order (A = most northern, F = most southern site).

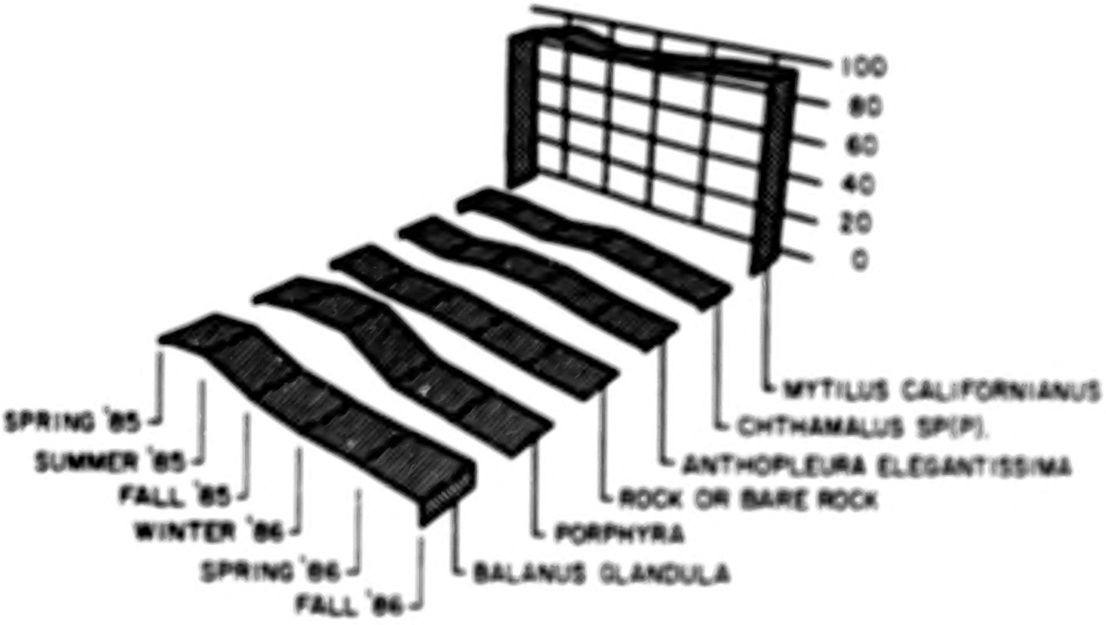


Figure I-9. *Mytilus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Kibesillah Hill (A).

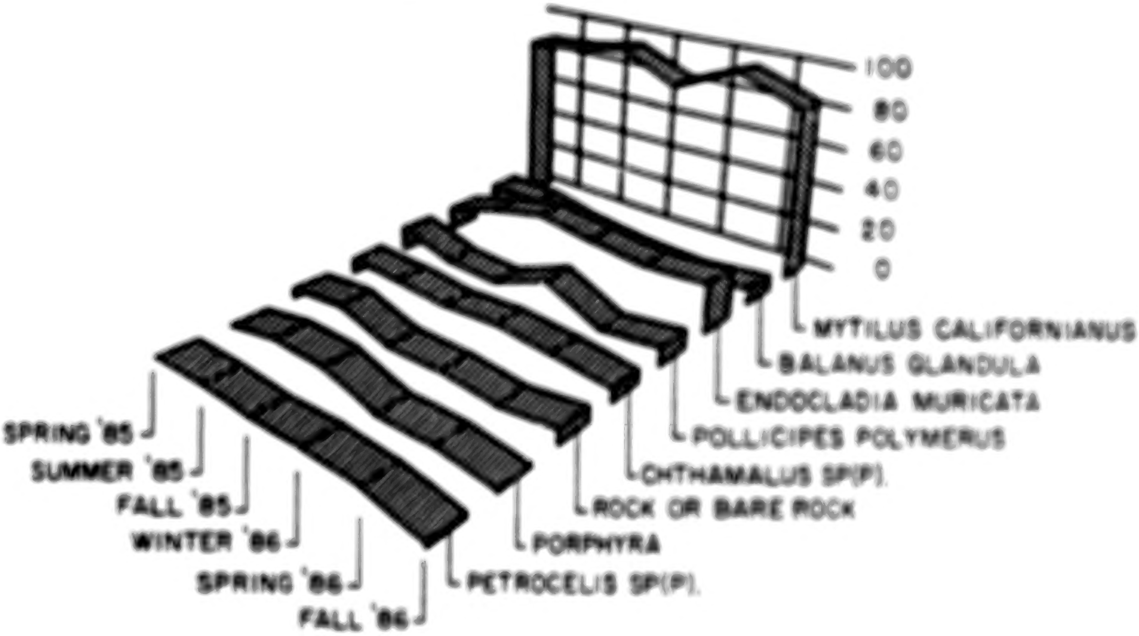


Figure I-10. *Mytilus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Sea Ranch (B).

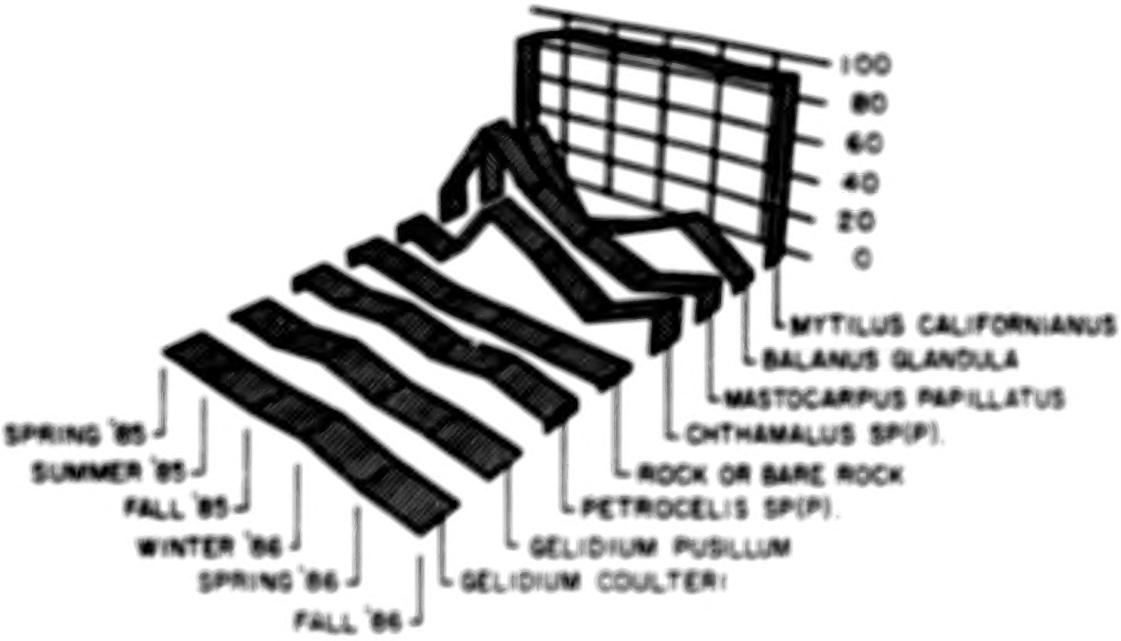


Figure I-11. *Mytilus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Bolinas (C).

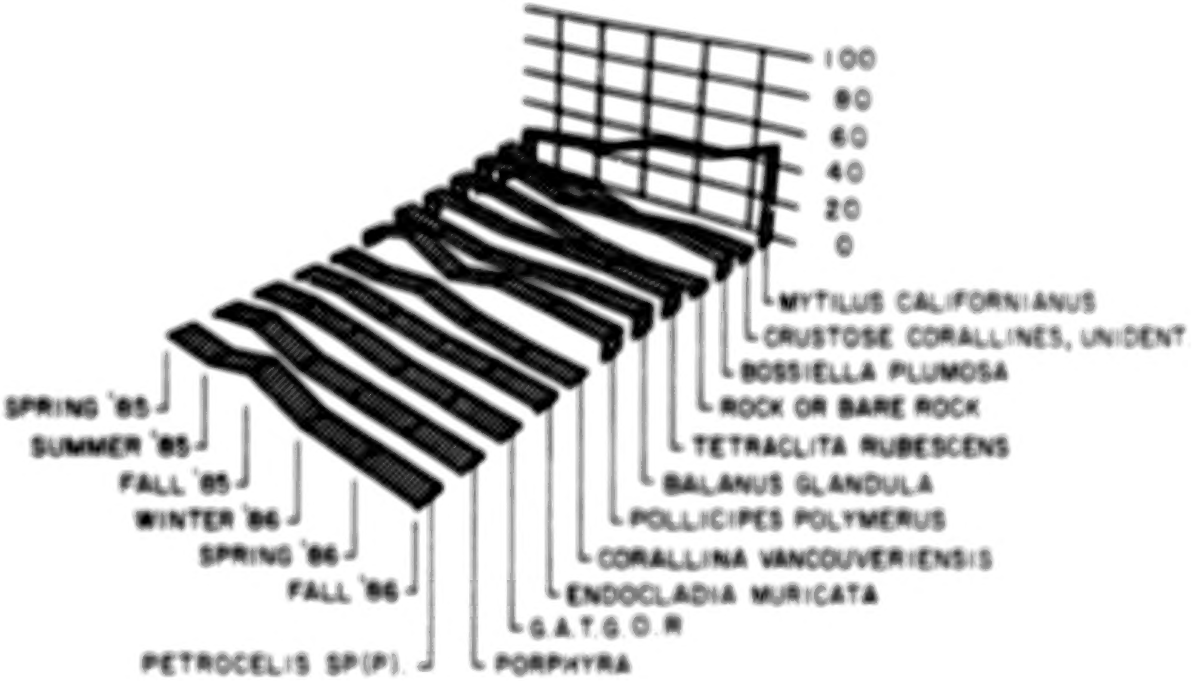


Figure I-12. *Mytilus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Pescadero Rocks (D).

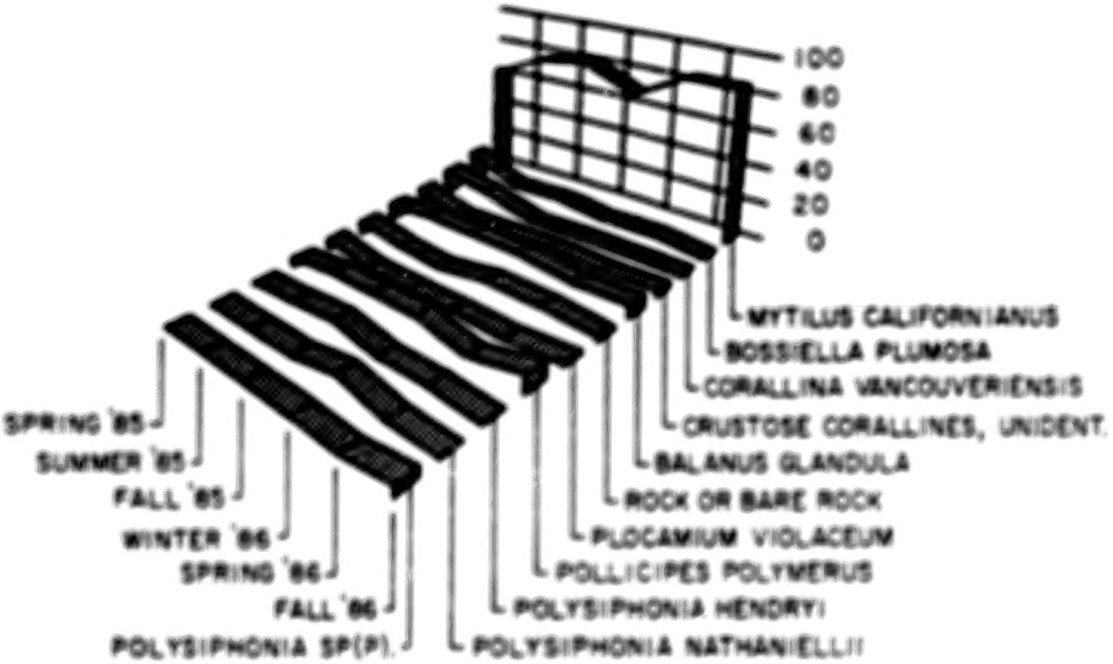


Figure I-13. *Mytilus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Pt. Sierra Nevada (E).

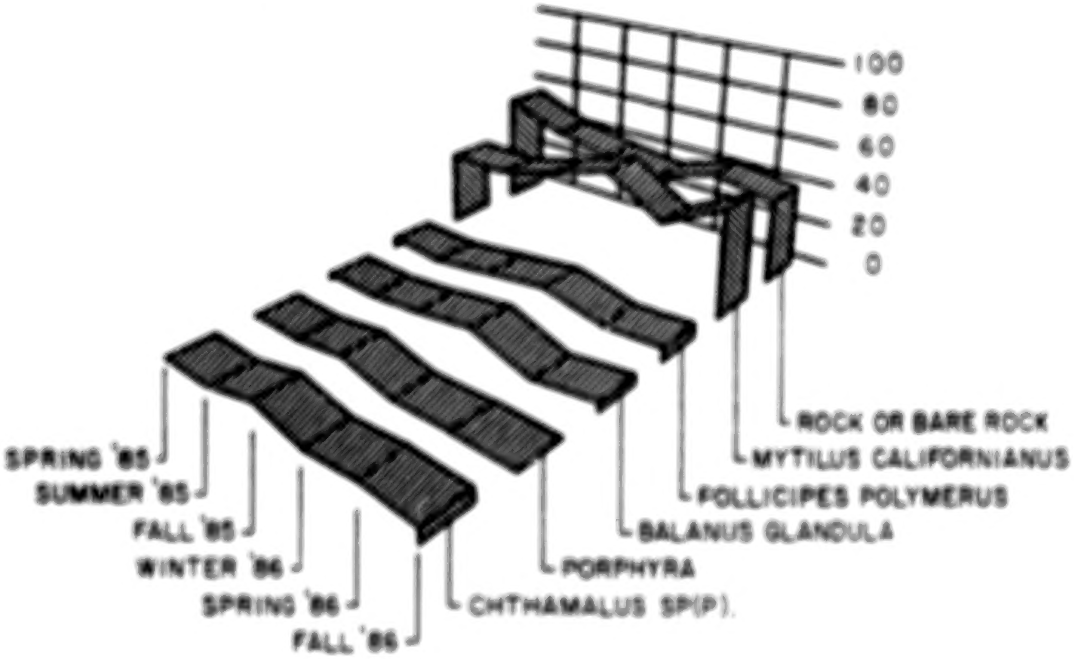


Figure I-14. *Mytilus* Assemblage: Temporal Abundance Data for Control Plots (Mean of 3 Plots) - Diablo Canyon (F).

Table I-7. Abundance (Counts) of the Dominant Motile Species in the *Mytilus* Assemblage Control Plots, Spring 1985 - Fall 1986. Mean* (Standard Deviation).

Name	Sampling Period	Kibesillah Hill (A)		Sea Ranch (B)		Bolinas (C)		Pescadero Rocks (D)		Pt. Sierra Nevada (E)		Diablo Canyon (F)	
CHITONS													
	Spring 85	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)	29.67	(3.51)	10.67	(5.51)	6.33	(2.08)
	Summer 85	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)	36.67	(31.21)	6.33	(3.79)	11.33	(2.08)
	Fall 85	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	24.00	(14.53)	4.67	(5.51)	7.67	(2.08)
	Winter 86	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	20.00	(9.54)	6.00	(3.61)	5.00	(1.73)
	Spring 86	0.67	(0.58)	0.00	(0.00)	0.00	(0.00)	20.83	(14.84)	5.67	(6.66)	11.33	(3.21)
	Fall 86	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	11.67	(2.31)	2.00	(1.73)	6.00	(1.00)
GRAZER LIMPETS													
	Spring 85	25.25	(13.18)	90.75	(52.54)	7.33	(4.51)	97.42	(78.00)	13.08	(20.07)	124.00	(25.88)
	Summer 85	34.58	(11.02)	216.92	(39.75)	23.08	(4.19)	141.67	(93.22)	163.92	(47.30)	254.08	(83.19)
	Fall 85	91.08	(51.65)	167.58	(62.05)	29.58	(23.51)	127.75	(57.95)	138.17	(21.45)	229.42	(36.88)
	Winter 86	90.83	(36.34)	138.83	(101.73)	10.50	(6.95)	133.00	(73.88)	120.58	(31.08)	140.75	(38.79)
	Spring 86	86.25	(51.34)	118.58	(65.03)	6.83	(5.01)	63.33	(26.09)	72.92	(19.38)	189.50	(17.03)
	Fall 86	39.67	(21.91)	116.33	(101.34)	24.08	(18.79)	104.50	(28.40)	86.75	(43.43)	327.00	(65.43)
LITTORINA SCUTULATA/PLENA													
	Spring 85	12.00	(19.08)	0.00	(0.00)	38.25	(14.43)	20.83	(21.95)	0.00	(0.00)	1.67	(1.53)
	Summer 85	26.08	(23.38)	2.08	(3.61)	16.92	(11.88)	35.08	(30.51)	6.92	(11.13)	3.33	(5.77)
	Fall 85	14.58	(14.98)	2.42	(3.36)	96.92	(41.95)	6.92	(5.76)	5.08	(8.80)	5.00	(4.36)
	Winter 86	17.58	(3.91)	1.00	(1.73)	42.25	(33.58)	31.25	(27.24)	0.67	(1.15)	0.00	(0.00)
	Spring 86	22.00	(6.26)	0.00	(0.00)	18.67	(7.47)	2.08	(3.61)	0.67	(1.15)	2.67	(2.08)
	Fall 86	70.58	(28.59)	0.00	(0.00)	284.42	(213.00)	0.33	(0.58)	4.33	(3.06)	7.33	(10.12)
NUCELLA EMARGINATA													
	Spring 85	5.08	(6.23)	1.00	(1.00)	2.00	(1.00)	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)
	Summer 85	1.33	(2.31)	3.00	(2.65)	2.00	(1.73)	0.33	(0.58)	2.00	(3.46)	0.00	(0.00)
	Fall 85	2.00	(1.00)	8.25	(13.43)	4.67	(3.79)	0.00	(0.00)	3.67	(3.06)	0.00	(0.00)
	Winter 86	1.67	(1.53)	11.33	(14.74)	2.00	(0.00)	0.00	(0.00)	2.33	(0.58)	0.67	(0.58)
	Spring 86	1.33	(1.53)	1.33	(2.31)	3.00	(1.00)	0.00	(0.00)	1.33	(0.58)	2.42	(4.19)
	Fall 86	1.67	(1.53)	6.00	(4.36)	7.00	(1.73)	0.00	(0.00)	3.67	(1.53)	0.00	(0.00)
TEGULA FUNEBRALIS													
	Spring 85	24.67	(11.59)	0.00	(0.00)	27.00	(9.54)	0.00	(0.00)	5.50	(9.53)	0.00	(0.00)
	Summer 85	13.00	(6.08)	0.33	(0.58)	20.33	(11.50)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 85	31.00	(12.49)	3.00	(3.61)	41.08	(7.80)	0.00	(0.00)	1.00	(1.00)	0.00	(0.00)
	Winter 86	35.33	(12.90)	0.33	(0.58)	55.67	(17.50)	0.00	(0.00)	0.67	(1.15)	0.00	(0.00)
	Spring 86	10.33	(8.50)	0.67	(1.15)	26.33	(5.13)	0.00	(0.00)	0.67	(1.15)	0.00	(0.00)
	Fall 86	18.67	(14.22)	0.33	(0.58)	32.67	(2.52)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)

*Mean number of individuals per 3 plots [value for each plot based on (sum of counts for 3 quadrats) ÷ 0.1875 sq.m].

I-8. With the exception of Bolinas (C), the number of such taxa that showed significant seasonal variation was low (0-3), as was the number of taxa that varied significantly between years at all sites (0-5; Table I-8, Summary). Most taxa were more abundant in the fall (12 out of 16). There was little difference in abundance between years (six species were more abundant in 1985, seven in 1986). There are no obvious latitudinal trends in the number of taxa per site showing significant seasonal or annual variation. The cause of the high seasonal variability at Bolinas (C) is unknown.

Summary

During the two years of this study, all measures used (species composition, abundance, similarities) indicate that only a few species varied significantly and that the variation observed is not correlated with latitude.

2. **How long does a completely cleared area take to recover after this disturbance? How is recovery time and pattern of recovery (or lack thereof) affected by assemblage, site, latitude, and time of year of clearing?**

These questions are related to the successional processes in plots cleared in spring and fall 1985, in each assemblage (*Endocladia*/*Mastocarpus*, *Mytilus*) at each of the six sites. The recovery of the cleared plots is assessed relative to the taxonomic composition and abundance (substrate percent cover is excluded) of the control plots using the Bray-Curtis similarity index. The criterion for "complete" recovery is that the mean similarity of each of the three cleared plots to the control plots falls within the range of similarities of the control plots to each other at the same time. The mean similarity of each cleared plot to control plots represents the mean of three pairwise comparisons [e.g., for fall clearings (F) in a particular assemblage at a particular site, the comparisons would be F1 - C1, F1 - C2, and F1 - C3, in which C is a control plot]. The relationship between recovery and latitude is examined by comparing various characteristics in the recovery plots along the latitudinal site gradient.

The Year I report (KLI, 1986) discussed the results of the first sampling of the spring clearings (summer 1985). It was noted that there were two patterns of initial colonization in the *Endocladia*/*Mastocarpus papillatus* assemblage: some sites remained nearly bare with little algal cover [Pt. Sierra Nevada (E), Bolinas (C)] while the remainder had variable amounts of diatoms, other ephemeral algae, and invertebrates. This pattern may have been related to differences in exposure to water motion, substratum type, and/or grazing. There was no suggestion of a latitudinal gradient in very early succession in this assemblage. The *Mytilus* assemblage had three patterns: very low cover of ephemeral algae at Bolinas (C), high cover of GATGOR at Kibesillah Hill (A), and high cover of diatoms at the remaining sites. Species in control plots (other than mussels) were found in the clearings but their abundances were very low. Again, there was no suggestion of a latitudinal gradient in early recovery. The fall clearings were not done in the period covered by the Year I report.

The results below cover the period from spring 1985 through fall 1986. During this period the spring clearings were sampled four times (summer and fall 1985, spring and fall 1986) and were 18 months post-clearing at the last sampling. The fall clearings were sampled three times (winter, spring and fall 1986) and were 12 months post-clearing at the last sampling. Details of data analysis equations are given in Appendix B, abundance data for all taxa found are given in Appendix C, ranked abundances by site and sampling period are in Appendix D, and Bray-Curtis similarity values are in Appendix F. The

Table I-8. *Mytilus* Assemblage: p Values for Abundant Taxa in Control Plots with High Probability of Temporal Variation ($p \leq .099$, that there was no Temporal Difference).

Site	Species	Temporal Variable[1] Season[2]	Year[3]	Y x S[4]
Kibesillah Hill (A)	Sessile:			
	Chthamalus sp(p).	0.09 (S)		
	Balanus glandula		0.02 (86)	
	Mytilus californianus		0.08 (86)	
	Motile:			
	Chitons	0.08 (S)	0.08 (86)	0.08
	Grazer Limpets			0.04
	Tegula funebralis		0.09 (85)	
	Littorina scutulata/plena	0.05 (F)	0.02 (86)	0.07
	TOTAL SPECIES	3	5	3
Sea Ranch (B)	Sessile:			
	Mytilus californianus			0.02
	TOTAL SPECIES	0	0	1

Table I-8. Continued.

		Temporal Variable		
Site	Species	Season	Year	Y x S
Bolinas (C)	Sessile:			
	Mastocarpus papillatus	0.04 (F)	0.01 (85)	
	Chthamalus sp(p).	0.002 (F)	0.08 (85)	
	Balanus glandula	0.005 (S)		
	Motile:			
	Grazer Limpets	0.06 (F)		
	Tegula funebralis	0.03 (F)		
	Littorina scutulata/plena	0.03 (F)		
	Nucella emarginata	0.03 (F)		
	TOTAL SPECIES	7	2	1
Pescadero Rocks (D)	Sessile:			
	Crustose corallines	0.002 (85)[a]		
	Corallina vancouveriensis		0.06 (85)	
	Petrocelis sp.	0.05 (F)		0.04
	Mytilus californianus		0.02 (86)	
	Motile:			
	Littorina scutulata/plena		0.09 (85)	
	TOTAL SPECIES	1	4	1

Table I-8. Continued.

Site	Species	Temporal Variable Season	Year	Y x S
Point Sierra (E)	Sessile:			
	Corallina vancouveriensis	0.08 (S)[a]		0.08
	Motile:			
	Grazer Limpets	0.003 (F)		0.009
	Nucella emarginata	0.02 (F)		
	TOTAL SPECIES	3	0	2
Diablo Canyon (F)	Sessile:			
	Chthamalus sp(p).	0.06 (F)'	0.09 (86)[a]	0.02
	Motile:			
	Chitons			0.03
	Grazer Limpets	0.0008 (F)	0.01 (86)	
	TOTAL SPECIES	2	2	2

Table I-8. Continued.

SUMMARY

SEASONAL AND YEAR TO YEAR CHANGES VS. LATITUDE

Number of Taxa with High Probability of Difference in Abundance:

	Sites					
	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
Season	3	0	7	1	3	2
Year to Year	5	0	2	4	0	2

---

[1] From ANOVA's in Appendix E. A blank = $p > .099$

[2] Fall vs. Spring; numbers are p values.

[3] 1985 vs. 1986; numbers as in 2.

[4] Year-Season interaction; numbers as in 2.

[5] (85) 1985 > 1986

[6] (S) Spring > Fall

[7] (F) Fall > Spring

[8] (86) 1986 > 1985

Note: complete analyses for all significant ANOVA's on abundant taxa (Sessile: >10% cover at any site at any time; Motile: 15 individuals/m^2 at any site at any time) with significant probabilities are shown in Appendix E.

criteria for inclusion of a species in statistical analyses (high abundance) were the same as those used for the controls described above.

Endocladia/Mastocarpus papillatus Assemblage

Results

Spring Clearings. The total number of taxa found during succession in the spring clearings was highly variable, ranging from 18 [Point Sierra Nevada (E)] to 44 [Sea Ranch (B); Table I-9]. This variation appears unrelated to latitude but is positively correlated with the total number of taxa found in the control plots at each site (Table I-3, correlation coefficient $r = 0.918$, $p < 0.01$).

As pointed out earlier (KLI, 1986), there were clear differences in taxa composition among sites during early succession, particularly for taxa whose abundance was measured as cover. Bolinas (C) and Point Sierra Nevada (E) had very little cover, Diablo Canyon (F) and Kibesillah Hill (A) had a low cover of ephemeral species such as GATGOR, *Cladophora columbiana*, and *Ralfsia* sp(p)., and Pescadero Rocks (D) and Sea Ranch (B) had a high cover of ephemeral species including blue-green, green [*Enteromorpha* sp(p)., *Ulva* sp(p)., *Urospora penicilliformis*] and/or ephemeral red [*Porphyra* sp(p).] algae (Figures I-15 - I-20). Ephemeral species at the latter four sites generally declined by fall 1986, with the most recent species composition most similar to the control plots (see below). Initial species composition and early successional patterns show no particular trends along the latitudinal gradient.

Trends in the abundances of motile taxa counted in the plots are less clear, with considerable temporal and spatial variability (Table I-10). *Limpets* were especially abundant at Sea Ranch (B), Pescadero Rocks (D), and Diablo Canyon (F), and generally increased in abundance with time at these sites. *Littorina scutulata/plena* were so abundant at Bolinas (C), Pescadero Rocks (D), and Point Sierra Nevada (E) that at times their cover exceeded 10 percent (Figures I-17, I-18 and I-19). However, temporal changes in their abundance at these sites showed no consistent pattern.

Analysis of Bray-Curtis similarities show that the spring clearings at Kibesillah Hill (A) (Figure I-21) completely recovered by 12 months, and two of the three plots at Point Sierra Nevada (E) (Figure I-25) completely recovered by 18 months. Recovery at Point Sierra Nevada (E) may be an anomalous result of differences in similarity amongst the control plots caused by a large decline in *Endocladia muricata* in control plot EC2 in fall 1986 (Figure I-7). One cleared plot was within the range of the controls after 18 months at Diablo Canyon (F) (Figure I-26). None of the cleared plots at the remaining three sites were within the range of similarity of the controls after 18 months, but all were close at Bolinas (C) (Figure I-23).

A qualitative comparison of Figures I-21 to I-26 reveals no particular trends in recovery with latitude (see also Conclusions below). Qualitative comparisons do, however, suggest an apparent inverse relationship between the cover of ephemeral species and recovery rate: Diablo Canyon (F) (Figure I-20), Point Sierra Nevada (E) (Figure I-19), Kibesillah Hill (A) (Figure I-15) and Bolinas (C) (Figure I-17) had low cover of ephemeral species, while the cover of these species was high at the other two sites [Sea Ranch (B) and Pescadero Rocks (D); Figures I-16 and I-18]. There also seem to be inverse relationships between recovery (similarity to controls) and total number of taxa in the control plots (Table I-3), and recovery and the total number of taxa found in the cleared

Table I-9. Taxa Sampled in the *Endocladia/Mastocarpus papillatus* Assemblage Spring-Cleared Plots, Summer 1985 - Fall 1986.

SITE:	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
SPECIES						
Acanthina sp(p).						X
Amphipoda, unident.	X	X	X	X	X	X
Anelipus japonicus		X	X			
Anthopleura elegantissima	X	X				
Balanus glandula	X	X	X	X	X	X
Bangia fusco-purpurea				X		
Bossiella plumosa		X				
Brown blades				X		
Brown crusts					X	
Chaetomorpha linum				X		
Chrysophyta, unident.		X		X	X	
Chthamalus sp(p).	X	X	X	X	X	X
Cirratulidae, unident.			X			
Cirripedia, unident.	X				X	X
Cladophora columbiana	X		X	X		X
"Collisella" scabra	X	X	X	X	X	X
Colpomenia peregrina			X			
Colpomenia sinuosa	X					
Copepoda, unident.		X			X	
Crepidula adunca						X
Crustose corallines, unident.		X				
Cryptosiphonia woodii			X			
Cumagloia andersonii						X
Cyanophyta, unident.				X		
Cylindrocarpus rugosus			X	X		X
Diptera-Diptera larvae	X	X		X		
Endocladia muricata	X	X	X	X	X	X
Enteromorpha intestinalis				X		
Enteromorpha linza		X		X		
Enteromorpha sp(p).				X		
Fucus distichus	X	X	X			
G.A.T.G.O.R.	X	X		X	X	X
Gigartina leptorhynchos						X
Green filaments				X		
Halosaccion glandiforme		X				
Hemigrapsus nudus	X					
Insecta, unident.		X			X	
Iridaea cordata		X				
Iridaea flaccida			X	X		X
Lacuna sp(p).		X				
Lepidochitona dentiens		X		X		X
Lepidochitona hartwegii					X	

Table I-9. (Continued)

SITE:	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
SPECIES						
Littorina keenae	X					
Littorina scutulata/plena	X	X	X	X	X	X
Littorina sp(p).				X		
Lottia asmi		X	X			X
Lottia digitalis	X	X	X	X	X	X
Lottia gigantea				X		
Lottia limatula		X		X		X
Lottia paradigitalis	X	X	X	X		
Lottia pelta	X	X	X			
Lottia sp(p).	X	X	X	X	X	X
Mastocarpus papillatus	X	X	X	X		X
Mopalia muscosa						X
Mytilus californianus			X	X		
Nemertea, unident.	X					
Nucella emarginata	X	X	X			X
Nuttallina californica				X		
Ocenebra circumtexta		X				X
Pachygrapsus crassipes						X
Pagurus sp(p).		X	X			X
Pelvetia-Pelvetiopsis sp(p).	X	X	X	X		X
Petrocelis sp(p).		X	X			X
Pholadidae, unident.			X			
Phragmatopoma californica		X				
Pisaster ochraceus		X				
Porphyra lanceolata		X		X	X	
Porphyra perforata	X	X		X	X	X
Porphyra sp(p).		X		X		
Ralfsia sp(p).		X	X			X
Rhodoglossum affine		X				X
Scytosiphon lomentaria					X	
Tectura scutum		X				
Tegula brunnea	X					X
Tegula funebralis	X	X	X			X
Ulva californica				X		
Ulva lobata		X		X		
Ulva sp(p).				X		
Urospora penicilliformis		X		X		
TOTAL TAXA	26	44	28	38	18	33

KH = Kibesillah Hill, SR = Sea Ranch, B = Bolinas, PR = Pescadero Rocks, PSN = Pt. Sierra Nevada, DC = Diablo Canyon. (A-F) designate latitudinal order (A = most northern, F = most southern site).

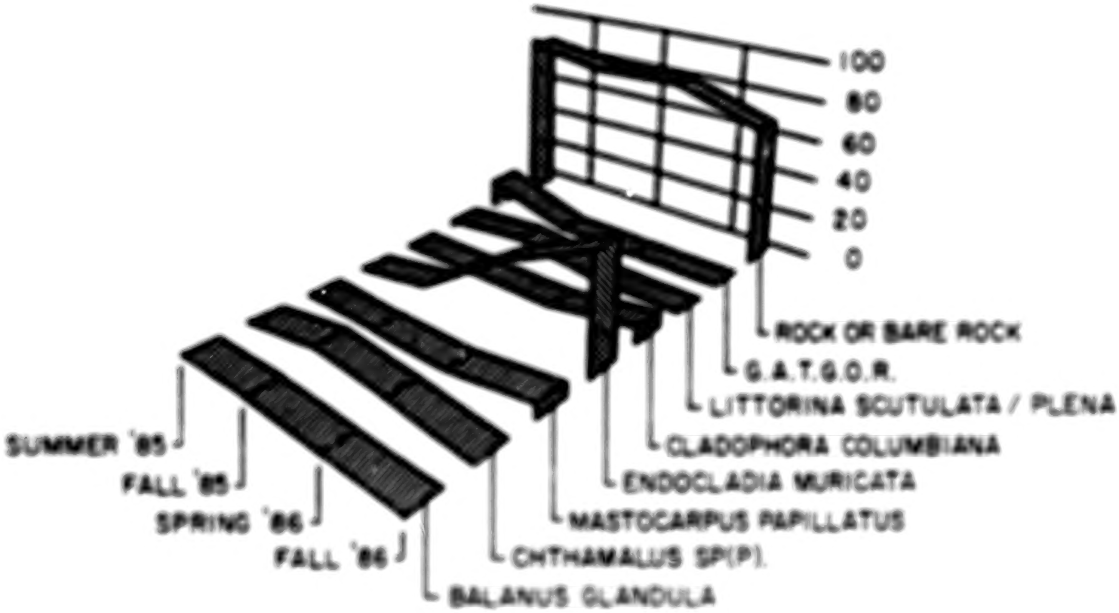


Figure I-15. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Kibesillah Hill (A).

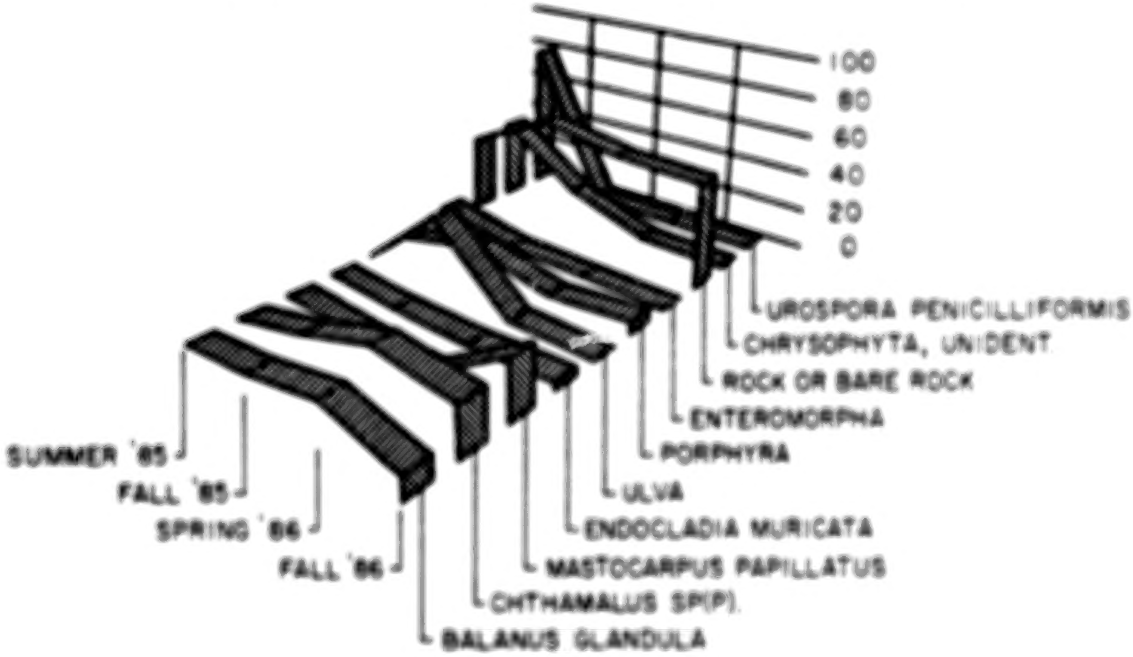


Figure I-16. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Sea Ranch (B).

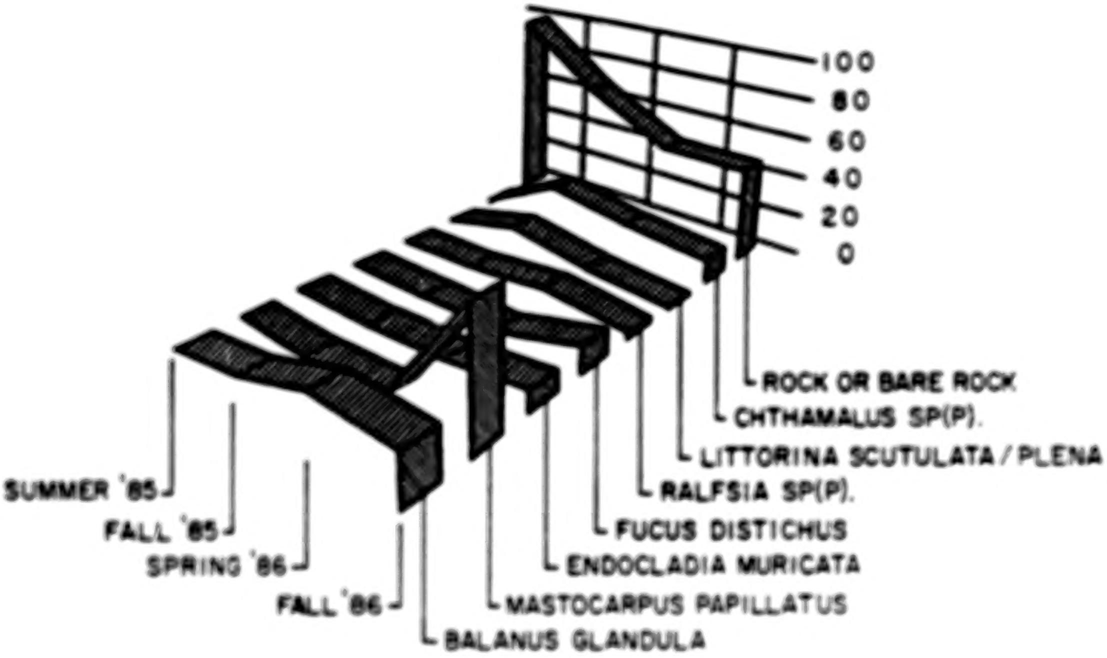


Figure I-17. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Bolinas (C).

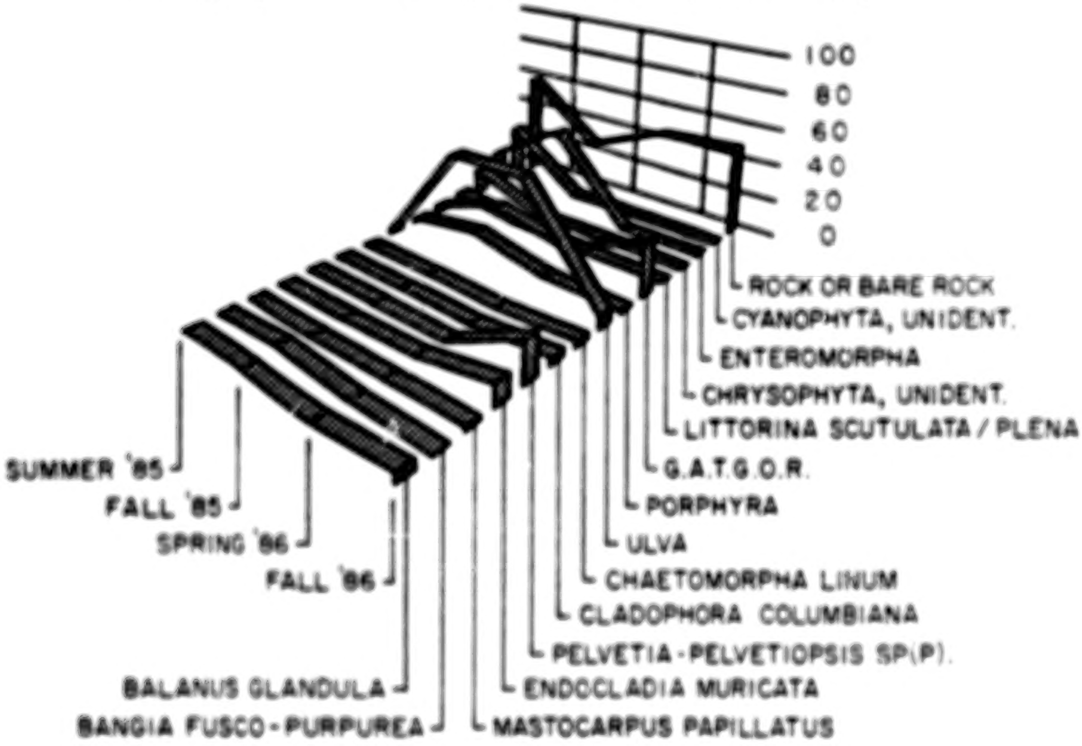


Figure I-18. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Pescadero Rocks (D).

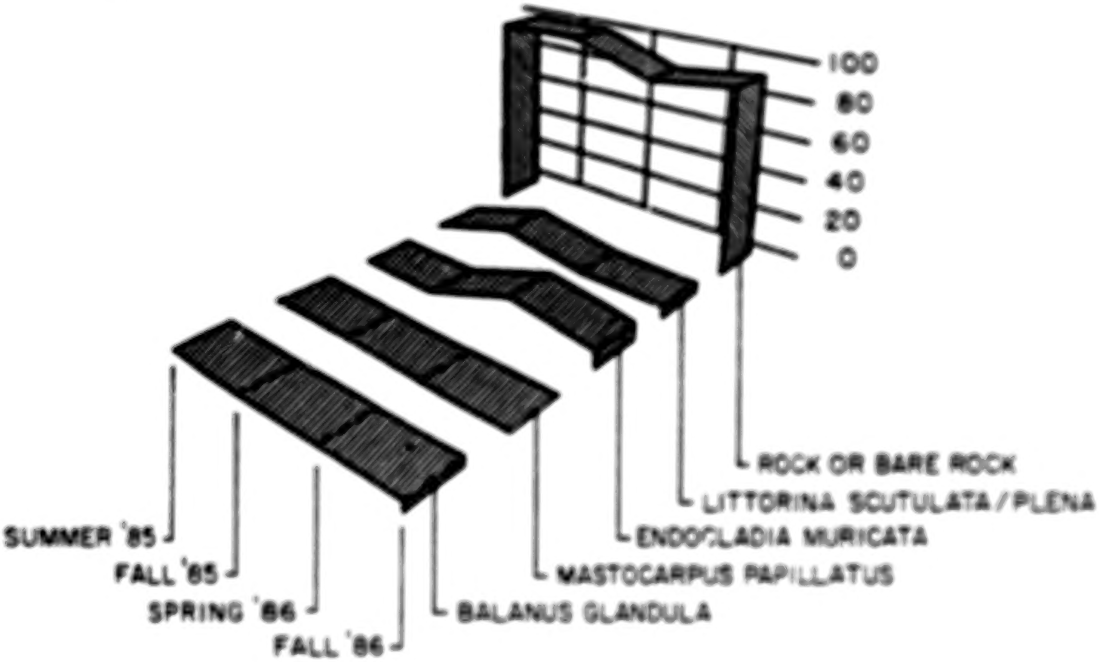


Figure I-19. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Pt. Sierra Nevada (E).

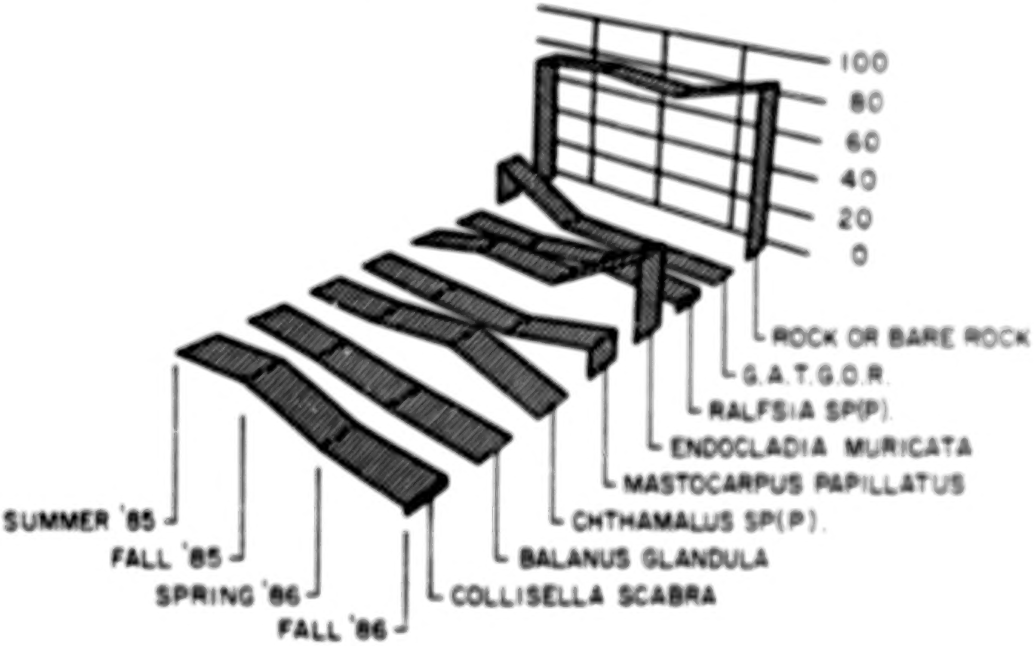


Figure I-20. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Diablo Canyon (F).

Table 1-10. Abundance (Counts) of the Dominant Motile Species in the *Endocladia/Mastocarpus papillatus* Assemblage Spring-cleared Plots, Summer 1985 - Fall 1986. Mean* (Standard Deviation).

Name	Sampling Period	Kibesillah Hill (A)		Sea Ranch (B)		Bolinas (C)		Pescadero Rocks (D)		Pt. Sierra Nevada (E)		Diablo Canyon (F)	
CHITONS													
	Summer 85	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 85	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.33	(0.58)
	Summer 86	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)	0.67	(1.15)	0.00	(0.00)	0.00	(0.00)
	Fall 86	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)	0.33	(0.58)	0.33	(0.58)	0.67	(1.15)
GRAZER LIMPETS													
	Summer 85	2.75	(4.76)	8.17	(10.87)	12.08	(16.67)	0.33	(0.58)	0.00	(0.00)	24.58	(10.10)
	Fall 85	36.83	(11.97)	14.25	(13.25)	10.42	(11.29)	41.75	(33.68)	0.33	(0.58)	300.92	(105.98)
	Spring 86	91.08	(66.48)	298.08	(74.55)	54.17	(56.94)	70.08	(29.11)	4.42	(1.66)	117.50	(42.43)
	Fall 86	62.92	(45.66)	198.67	(163.66)	54.92	(14.38)	232.67	(40.25)	6.08	(10.54)	114.08	(39.74)
LACUNA SP(P)													
	Summer 85	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 85	0.00	(0.00)	41.67	(72.17)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Summer 86	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 86	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
LITTORINA KEENAE													
	Summer 85	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 85	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Summer 86	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 86	27.08	(46.91)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
LITTORINA SCUTULATA/PLENA													
	Summer 85	95.67	(53.56)	1.33	(2.31)	157.17	(106.63)	858.25	(1086)	191.33	(122.65)	27.08	(42.65)
	Fall 85	556.50	(163.76)	28.08	(35.34)	741.83	(73.79)	1.00	(1.73)	536.75	(190.48)	13.33	(10.12)
	Spring 86	92.33	(34.81)	91.67	(158.77)	590.08	(249.45)	462.00	(553.12)	494.75	(134.05)	123.42	(79.08)
	Fall 86	122.67	(41.23)	150.58	(149.98)	642.00	(230.32)	131.92	(190.02)	564.42	(239.03)	0.00	(0.00)
LITTORINA SP(P).													
	Summer 85	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 85	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	77.08	(133.51)	0.00	(0.00)	0.00	(0.00)
	Summer 86	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 86	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
NUCELLA EMARGINATA													
	Summer 85	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 85	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Summer 86	0.33	(0.58)	1.33	(1.15)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	1.67	(1.15)
	Fall 86	0.33	(0.58)	0.33	(0.58)	1.00	(1.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
TEGULA FUNEBRALIS													
	Summer 85	1.00	(1.73)	3.33	(1.15)	7.00	(6.56)	0.00	(0.00)	0.00	(0.00)	19.33	(19.86)
	Fall 85	0.33	(0.58)	3.67	(3.51)	3.00	(3.00)	0.00	(0.00)	0.00	(0.00)	8.00	(13.86)
	Spring 86	3.00	(3.00)	3.08	(4.33)	5.33	(7.51)	0.00	(0.00)	0.00	(0.00)	4.33	(4.51)
	Fall 86	5.33	(3.51)	1.00	(1.00)	12.33	(3.21)	0.00	(0.00)	0.00	(0.00)	28.33	(30.89)

*Mean number of individuals per 3 plots (value for each plot based on (sum of counts for 3 quadrats) #/0.1875 sq.m).

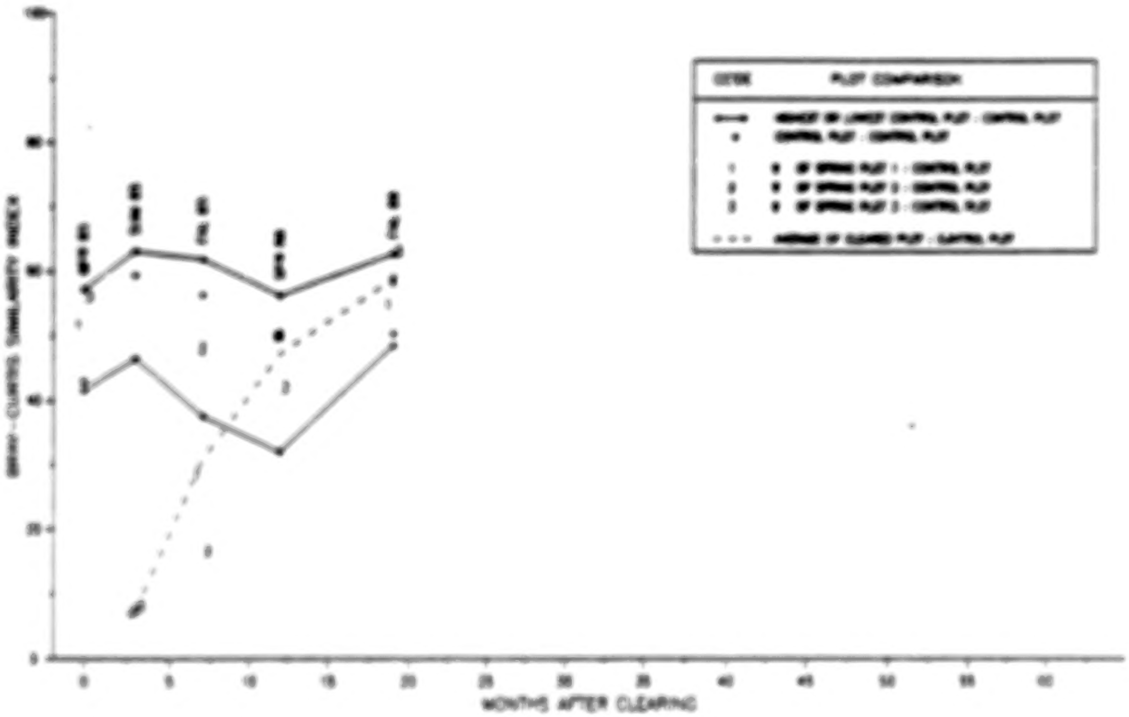


Figure 1-21. *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots through Time - Kibesillah Hill (A).

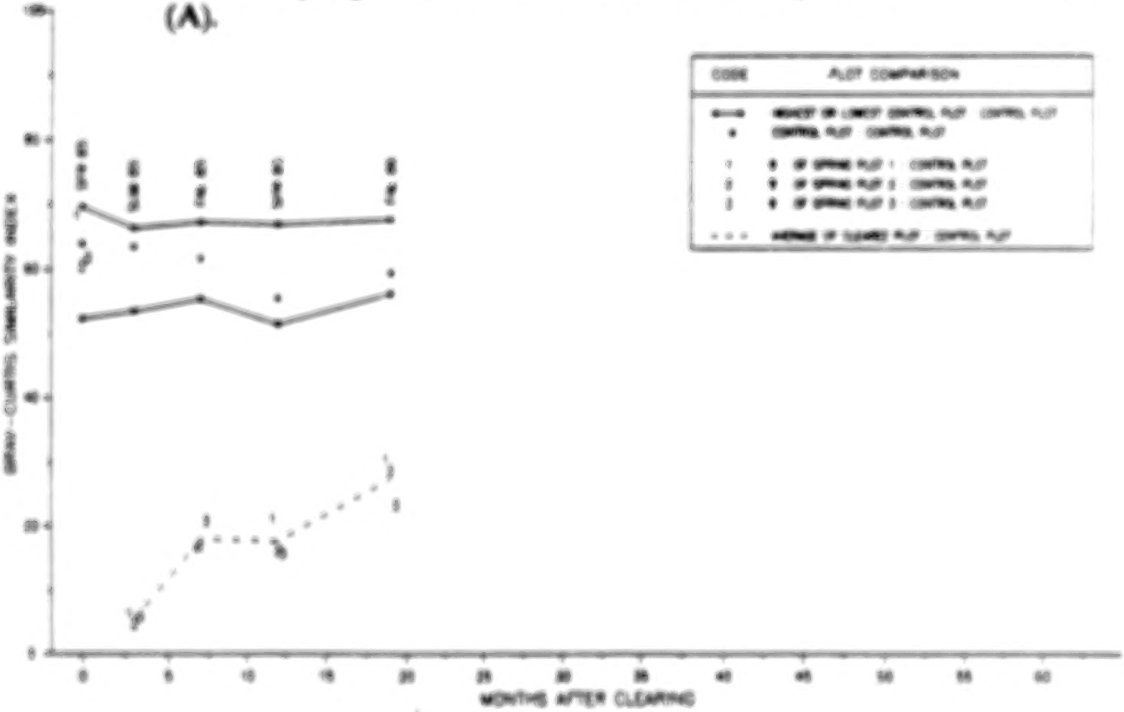


Figure 1-22. *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots through Time - Sea Ranch (B).

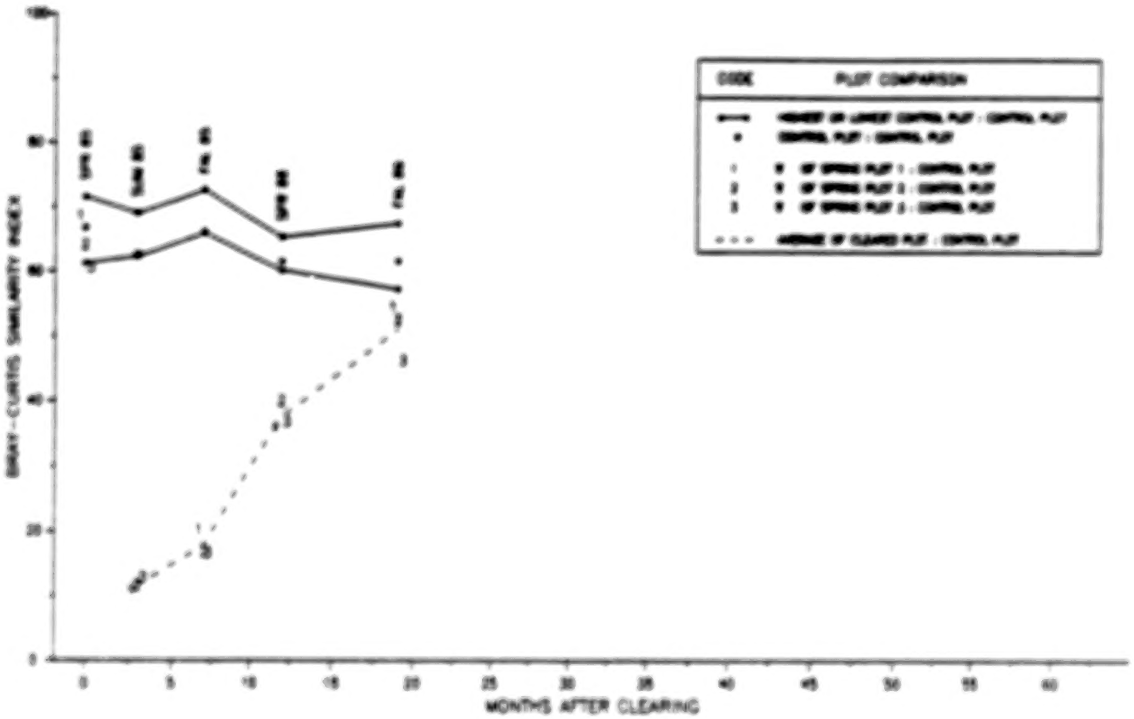


Figure I-23. *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots through Time - Bolinas (C).

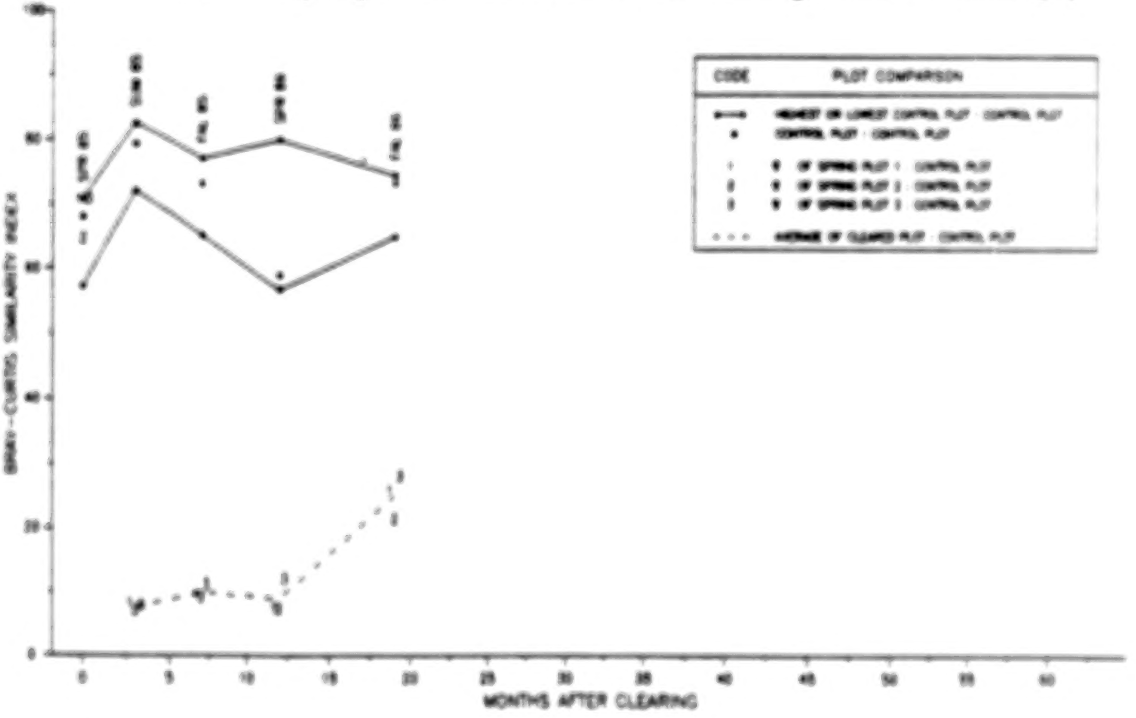


Figure I-24. *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots through Time - Pescadero Rocks (D).

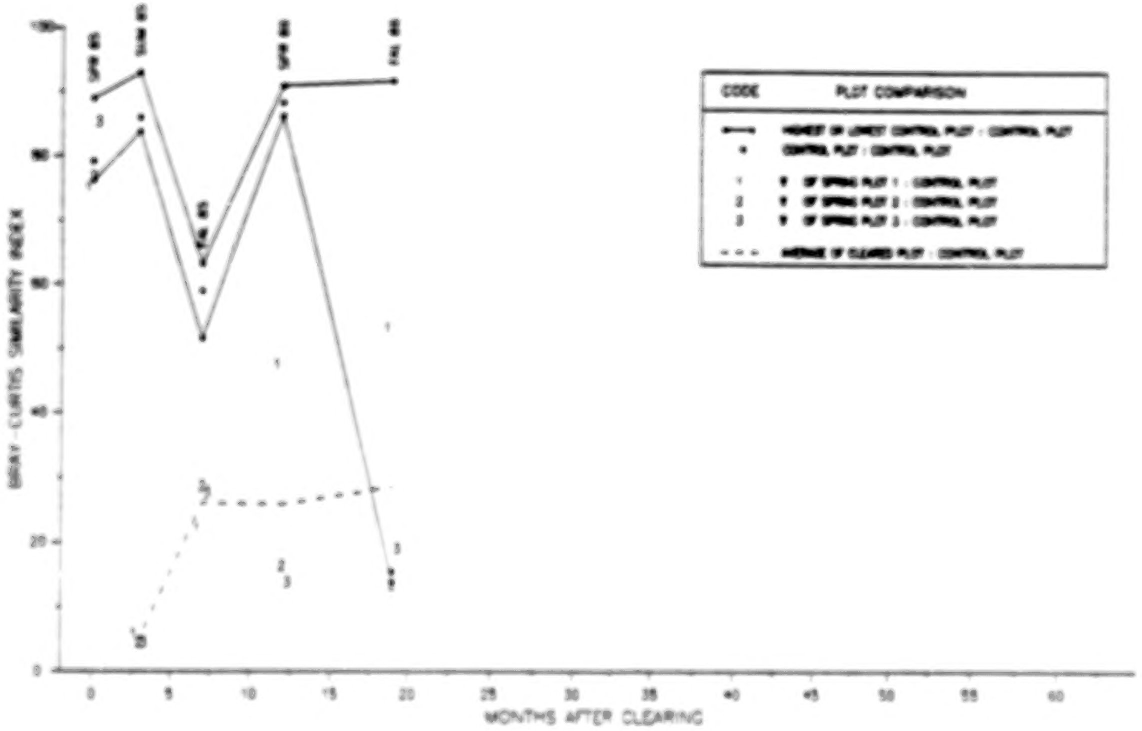


Figure I-25. *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots through Time - Pt. Sierra Nevada (E).

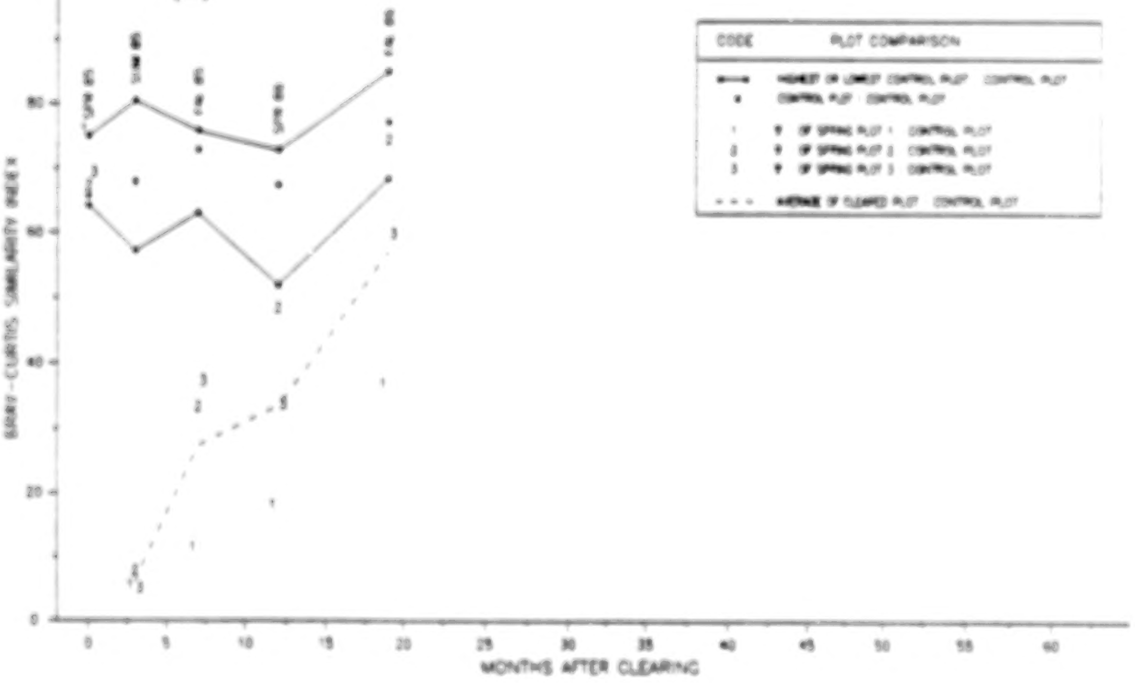


Figure I-26. *Endocladic/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots through Time - Diablo Canyon (F).

plots (Table I-9). As most ephemeral taxa have persisted in low abundance, the latter relationship may simply reflect the presence of these taxa in cleared plots only (reducing similarity to controls that do not have these species), and not differences between taxa common to both cleared and control plots. These relationships will be quantitatively examined in the next report.

Fall Clearings. As might be expected because of differences in time since clearing, the fall-cleared plots had accumulated fewer taxa by the last sampling than had the spring-cleared plots; Point Sierra Nevada (E) is the exception [25 species in fall clearings (Table I-11) vs. 18 in spring clearings (Table I-9)]. There is no latitudinal trend in number of taxa per site and no significant correlation between number of taxa in clearings and number of taxa in controls (Table I-3 vs. Table I-11; correlation coefficient $r = 0.584$, $p>0.5$) at 12 months.

Patterns of abundance (cover) of ephemeral taxa (Figures I-27 - I-32) were similar to those in the spring clearings, with diatoms, *Ulva* sp(p)., *Enteromorpha* sp(p)., *Urospora penicilliformis*, *Ralfsia* sp(p)., and *Porphyra* sp(p). most abundant at Pescadero Rocks (D) (Figure I-30) and Sea Ranch (B) (Figure I-28), and least abundant at Bolinas (C) (Figure I-29), Diablo Canyon (F) (Figure I-32), Point Sierra Nevada (E) (Figure I-31), and Kibesillah Hill (A) (Figure I-27). In general, the overall species composition of ephemerals was similar to that in the spring clearings, as was the composition and abundance of species within sites [e.g., *Ulva* sp(p). at Pescadero Rocks (D), *Urospora* sp(p). at Sea Ranch (B)]. With the exception of *Ulva* sp(p). at Pescadero Rocks (D), ephemeral algae had declined by fall 1986, 12 months after clearing. There were no apparent latitudinal trends in the species composition and abundance of ephemerals.

There were fewer dominant motile fauna counted in the fall-cleared plots (Table I-12) than in the spring-cleared plots (Table I-10) at the same post-clearing age. The taxa absent from the fall plots were those that were rare in the spring plots [*Lacuna* sp(p). and *Littorina* sp(p).]. With the exception of the low abundance of *Littorina scutulata/plena* in fall clearings at Pescadero Rocks (D), the relative abundance of this taxon, limpets, and *Tegula funebralis* among sites was similar in fall and spring. These data show no consistent temporal or latitudinal trends in the abundance of motile animal species.

At 12 months after clearing, only the fall cleared plots in the *Endocladia/Mastocarpus papillatus* assemblage at Point Sierra Nevada (E) (Figure I-37) were completely recovered. However, as discussed above for the spring-cleared plots at this site, this high similarity is associated with changes in one of the control plots. None of the cleared plots at the other sites were within the range of control similarities (Figures I-33, I-34, I-35, I-36, I-38), but those at Bolinas (C) were all very close (Figure I-35). Because of the generally and uniformly low similarities between the fall clearings and controls, there are no obvious qualitative relationships between recovery rate and cover of ephemeral species or other variables as there were in the spring clearings. These relationships will be examined if continued succession produces differences in recovery rate.

Summary

After eighteen months of succession, the spring-cleared plots in the *Endocladia/Mastocarpus papillatus* assemblage at one site, Kibesillah Hill (A), have completely recovered. Two of the three plots at Point Sierra Nevada and one of the plots at Diablo Canyon (F) have also recovered. After twelve months, the only complete recovery of fall clearings has been at Point Sierra Nevada (E); none of the fall-cleared

Table I-11. Taxa Sampled in the *Endocladia/Mastocarpus papillatus* Assemblage Fall-Cleared Plots, Winter 1986 - Fall 1986.

SITE:	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
SPECIES						
Acanthina sp(p).			X			
Amphipoda, unident.	X	X	X	X	X	X
Analipus japonicus		X	X			
Anthopleura elegantissima	X					
Balanus glandula	X	X	X		X	
Bangia fusco-purpurea		X				
Brown crusts					X	
Chaetomorpha linum				X		
Chrysophyta, unident.		X	X	X	X	
Chthamalus sp(p).	X	X	X		X	
Cladophora columbiana		X	X			
"Collisella" scabra	X	X	X	X	X	X
Colpomenia sinuosa			X			
Colpomenia sp(p).					X	
Copepoda, unident.				X		X
Corallina vancouveriensis						X
Crepidula adunca						X
Crustose corallines, unident.		X			X	X
Cumagloia andersonii						X
Cylindrocarpus rugosus						X
Diptera-Diptera larvae		X		X		
Endocladia muricata	X			X	X	X
Enteromorpha linza				X		
Enteromorpha sp(p).				X		
Fucus distichus			X			
G.A.T.G.O.R.				X	X	
Gigartina leptorhynchos						X
Green blades				X		
Green filaments		X				
Halosaccion glandiforme		X				
Iridaea flaccida		X				X
Isopoda, unident.	X	X	X			
Lepidochitona dentiens					X	
Lepidochitona hartwegii				X		
Littorina scutulata/plena	X	X	X	X	X	X
Littorina sp(p).						X
Lottia asmi			X			X
Lottia digitalis	X	X	X	X	X	X
Lottia gigantea					X	
Lottia limatula		X		X	X	X
Lottia paradigitalis	X	X	X	X		
Lottia pelta	X	X		X	X	X
Lottia sp(p).	X	X	X	X	X	X

Table I-11. (Continued)

SITE:	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
SPECIES						
Mastocarpus papillatus	X	X	X	X	X	X
Nemertea, unident.	X					
Nucella emarginata	X	X			X	X
Nuttallina californica						X
Pachygrapsus crassipes						X
Pagurus sp(p).			X		X	X
Pelvetia-pelvetiopsis sp(p).				X		
Petrocelis sp(p).	X	X	X			X
Phragmatopoma californica						X
Porphyra lanceolata	X	X		X	X	
Porphyra perforata	X	X	X	X	X	X
Porphyra sp(p).	X	X	X	X	X	
Pterosiphonia bipinnata			X			
Ralfsia sp(p).			X			X
Red blades			X			
Tectura scutum						X
Tegula brunnea					X	
Tegula funebralis	X	X	X		X	X
Ulva lobata				X		
Ulva sp(p).		X		X		
Urospora penicilliformis				X		
Urospora wormskioldii		X				
TOTAL TAXA	20	29	25	26	25	29

KH = Kibesillah Hill, SR = Sea Ranch, B = Bolinas, PR = Pescadero Rocks, PSN = Pt. Sierra Nevada, DC = Diablo Canyon. (A-F) designate latitudinal order (A = most northern, F = most southern site).

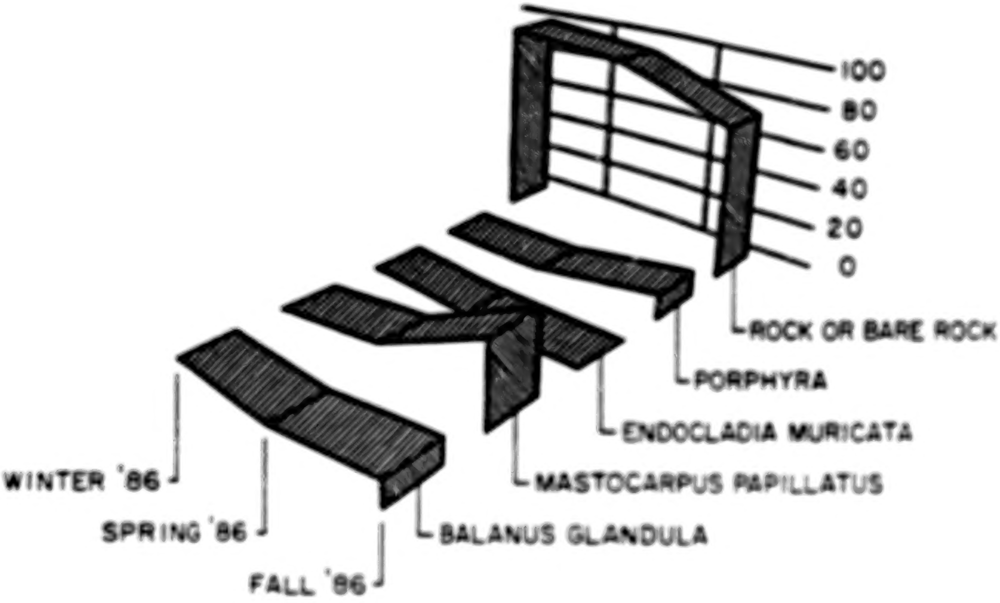


Figure I-27. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Kibesillah Hill (A).

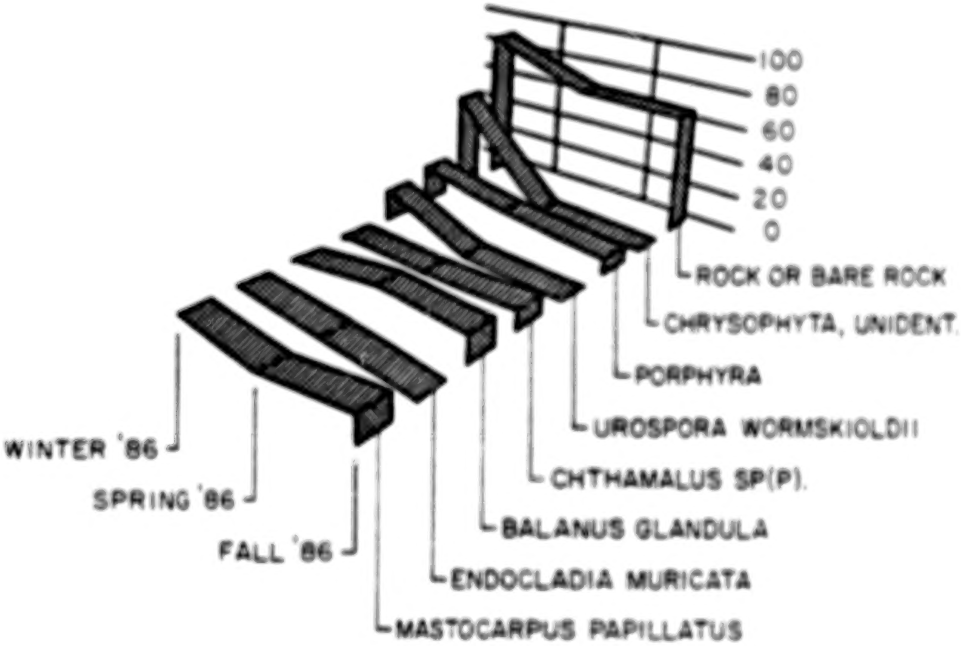


Figure I-28. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Sea Ranch (B).

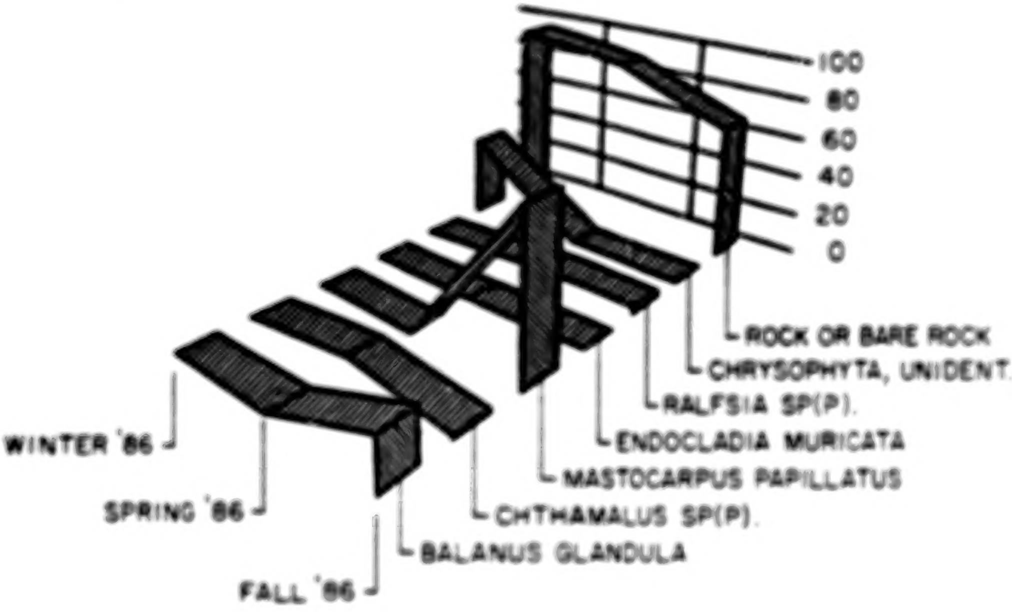


Figure 1-29. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Bolinas (C).

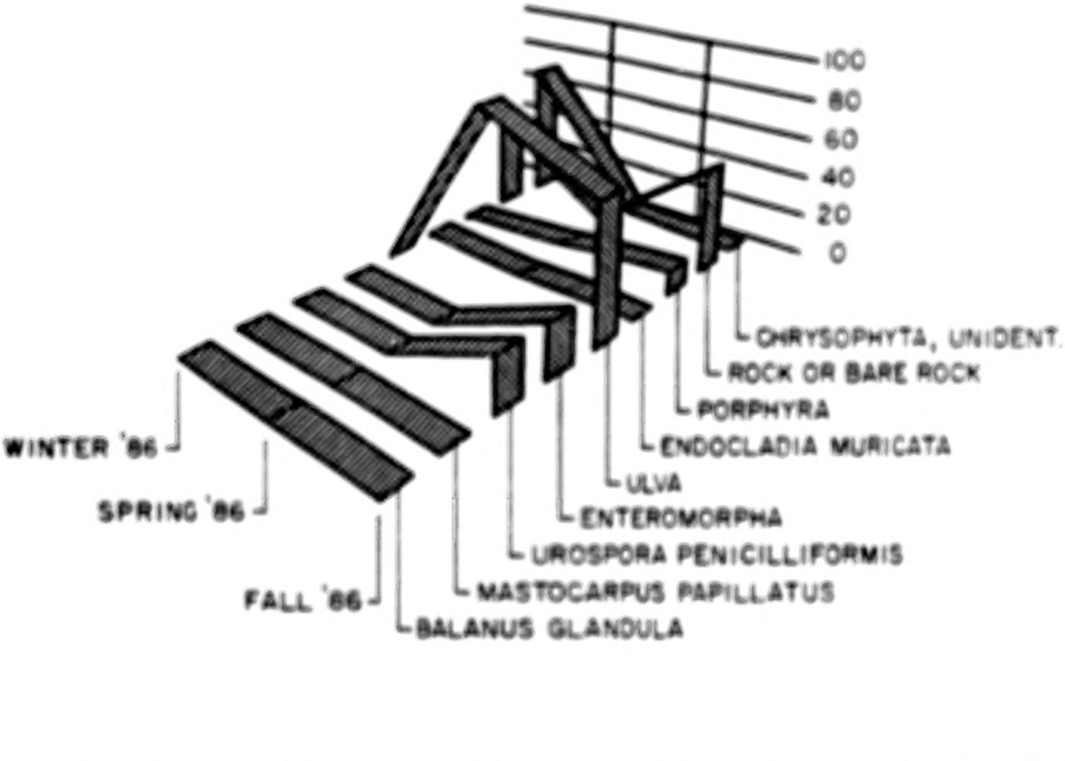


Figure 1-30. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Pescadero Rocks (D).

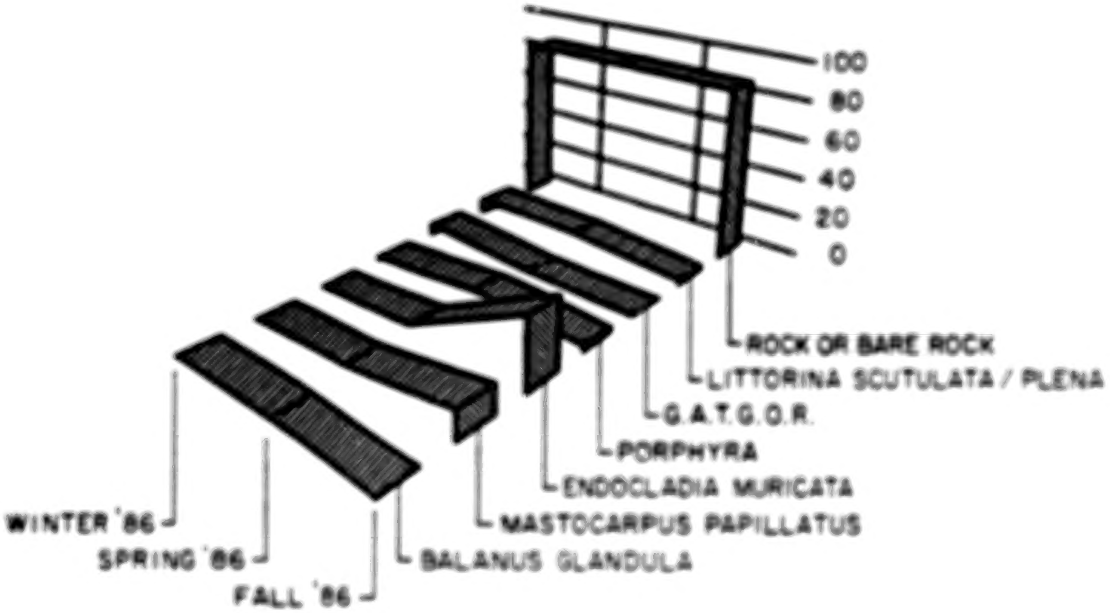


Figure 1-31. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Pt. Sierra Nevada (E).

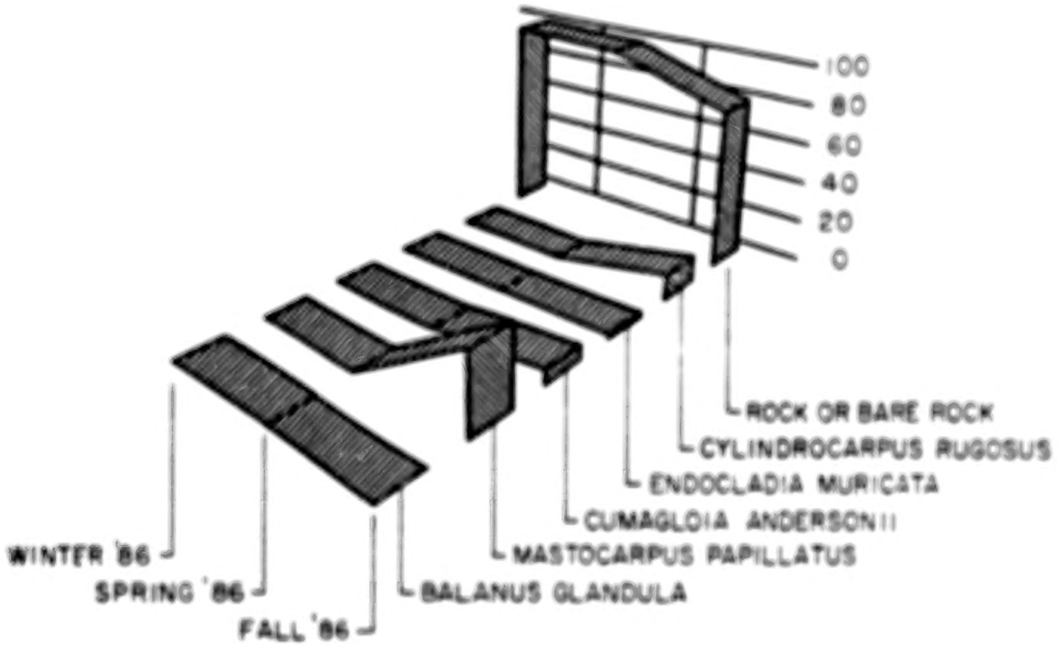


Figure 1-32. *Endocladia/Mastocarpus papillatus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Diablo Canyon (F).

Table I-12. Abundance (Counts) of the Dominant Motile Species in the *Endocladia/Mastocarpus papillatus* Assemblage Fall-cleared Plots, Winter 1986 - Fall 1986. Mean* (Standard Deviation).

Name	Sampling Period	Kibesillah Hill (A)		Sea Ranch (B)		Bolinas (C)		Pescadero Rocks (D)		Pt. Sierra Nevada (E)		Diablo Canyon (F)	
CHITONS													
	Winter 86	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.33	(0.58)
	Spring 86	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)
	Fall 86	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)	0.00	(0.00)
GRAZER LIMPETS													
	Winter 86	41.83	(11.22)	3.00	(2.65)	3.75	(3.95)	0.33	(0.58)	0.67	(0.58)	5.33	(2.31)
	Spring 86	132.50	(84.38)	56.25	(70.15)	2.00	(0.00)	2.75	(4.76)	1.67	(0.58)	5.42	(7.65)
	Fall 86	41.08	(31.25)	287.67	(178.80)	10.67	(7.95)	107.08	(115.24)	5.75	(3.31)	77.00	(18.33)
LITTORINA SCUTULATA/PLENA													
	Winter 86	604.85	(919.41)	3.33	(0.58)	179.58	(103.32)	0.00	(0.00)	500.92	(252.21)	60.75	(84.83)
	Spring 86	573.18	(352.60)	36.42	(17.24)	433.75	(120.47)	0.00	(0.00)	656.92	(159.50)	164.58	(190.96)
	Fall 86	514.42	(741.18)	12.17	(7.11)	290.08	(105.73)	14.92	(15.67)	877.42	(84.17)	0.00	(0.00)
NUCELLA EMARGINATA													
	Winter 86	0.00	(0.00)	1.00	(1.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	1.00	(1.00)
	Spring 86	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.33	(0.58)
	Fall 86	2.00	(1.73)	2.67	(2.31)	0.00	(0.00)	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)
TEGULA FUNEBRALIS													
	Winter 86	6.67	(8.08)	6.33	(10.12)	6.33	(1.53)	0.00	(0.00)	4.33	(6.66)	88.75	(78.98)
	Spring 86	3.33	(3.51)	4.33	(6.66)	2.67	(3.06)	0.00	(0.00)	0.33	(0.58)	42.67	(71.32)
	Fall 86	6.33	(5.69)	7.67	(6.35)	15.67	(3.21)	0.00	(0.00)	2.33	(4.04)	27.33	(11.50)

*Mean number of individuals per 3 plots [value for each plot based on (sum of counts for 3 quadrats) #/0.1875 sq.m).

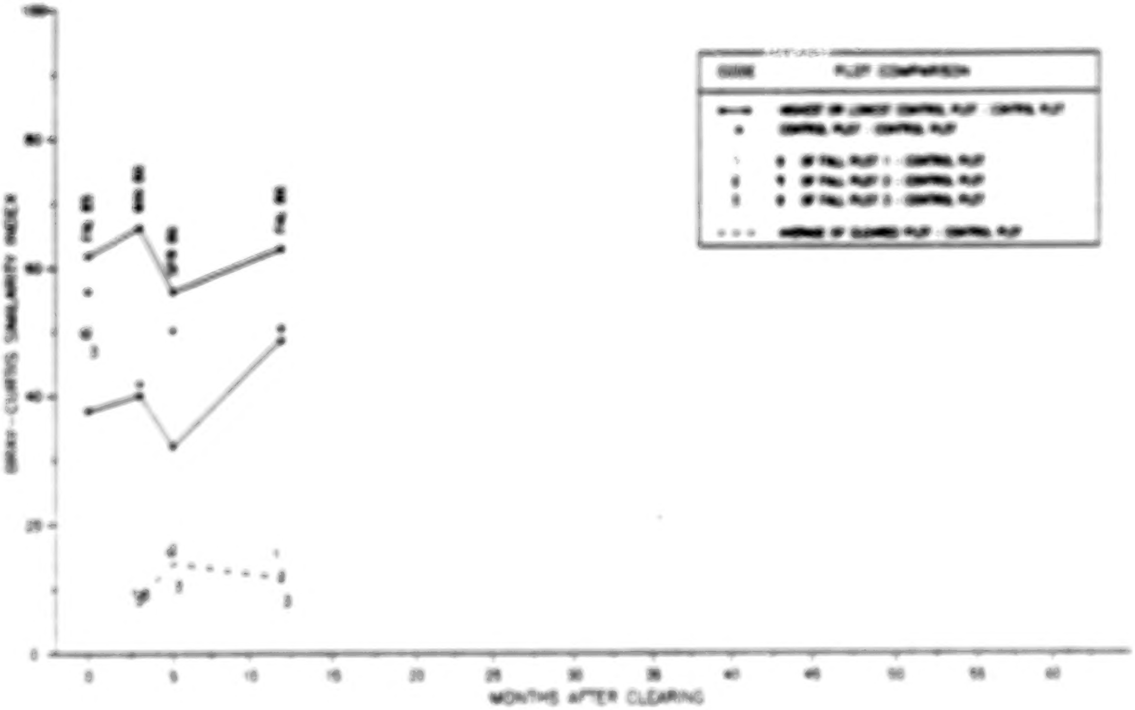


Figure I-33. *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Kibesillah Hill (A).

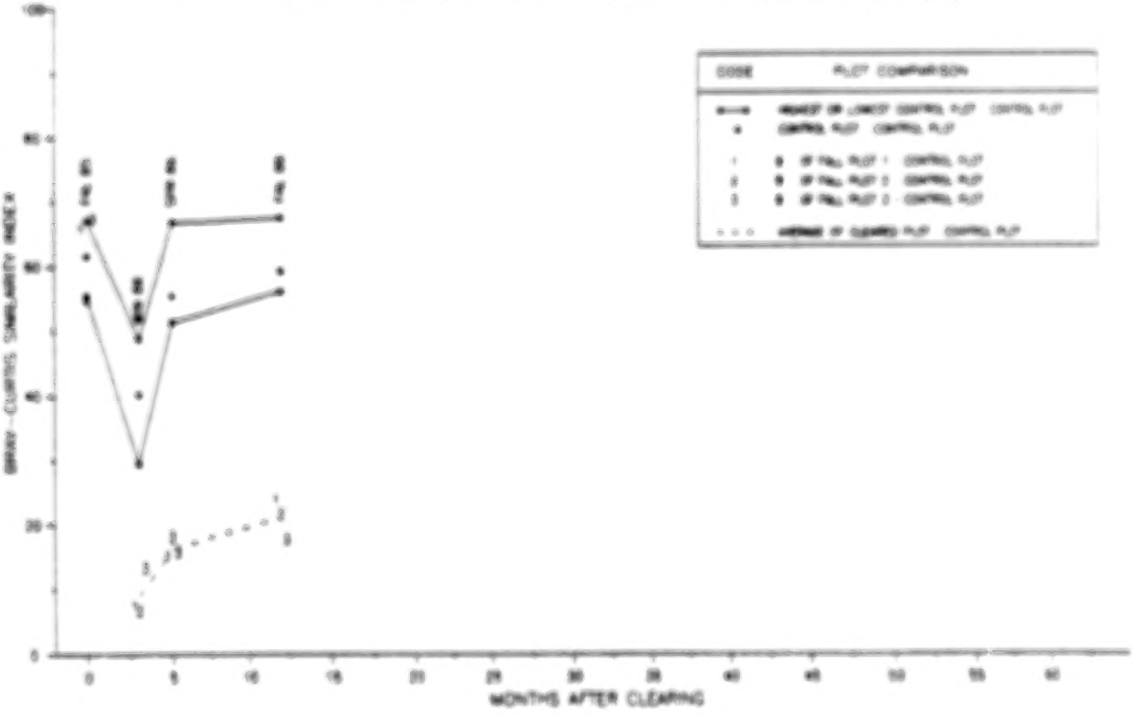


Figure I-34. *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Sea Ranch (B).

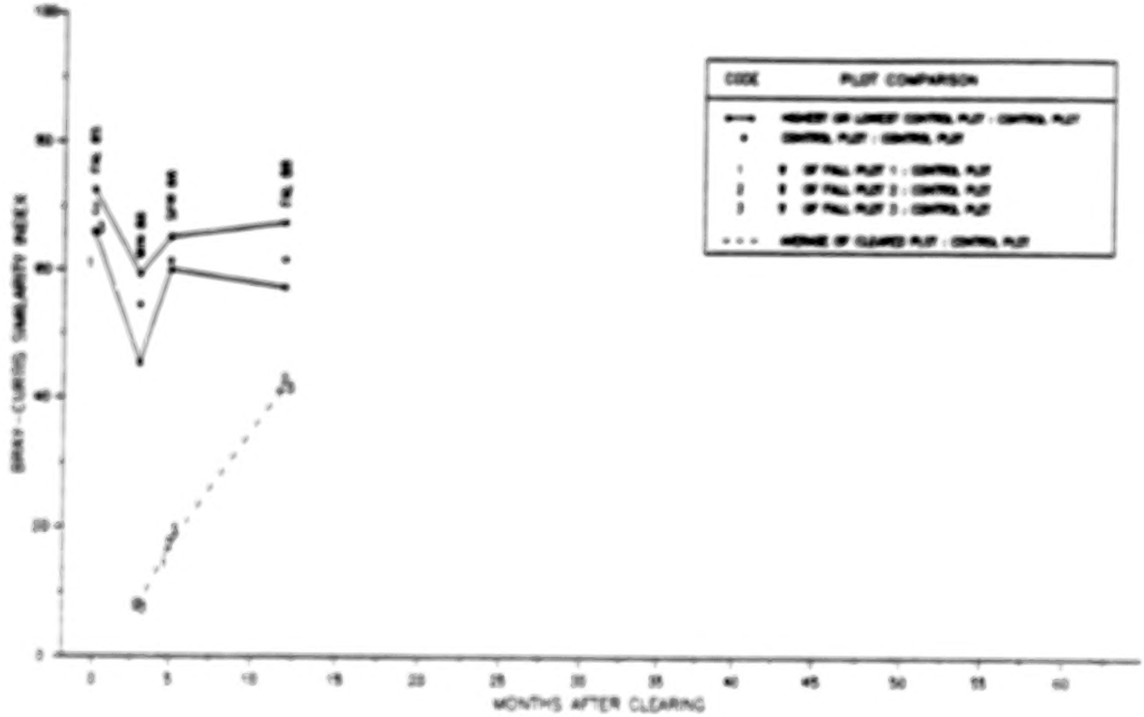


Figure I-35. *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Bolinas (C).

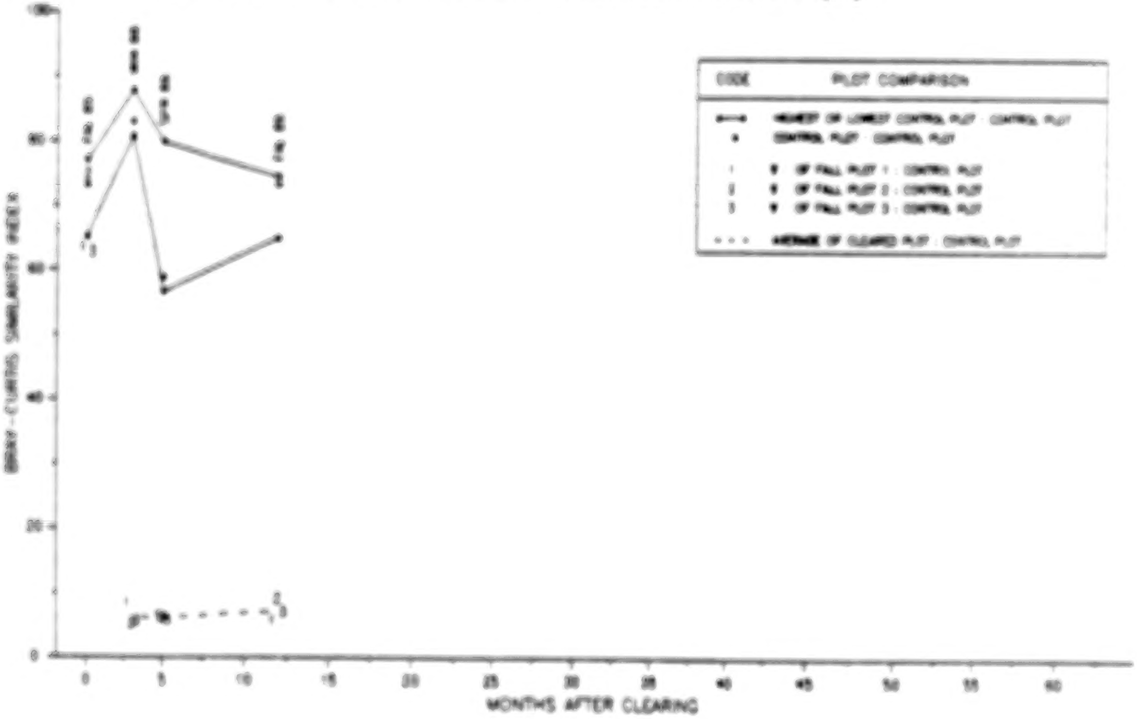


Figure I-36. *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Pescadero Rocks (D).

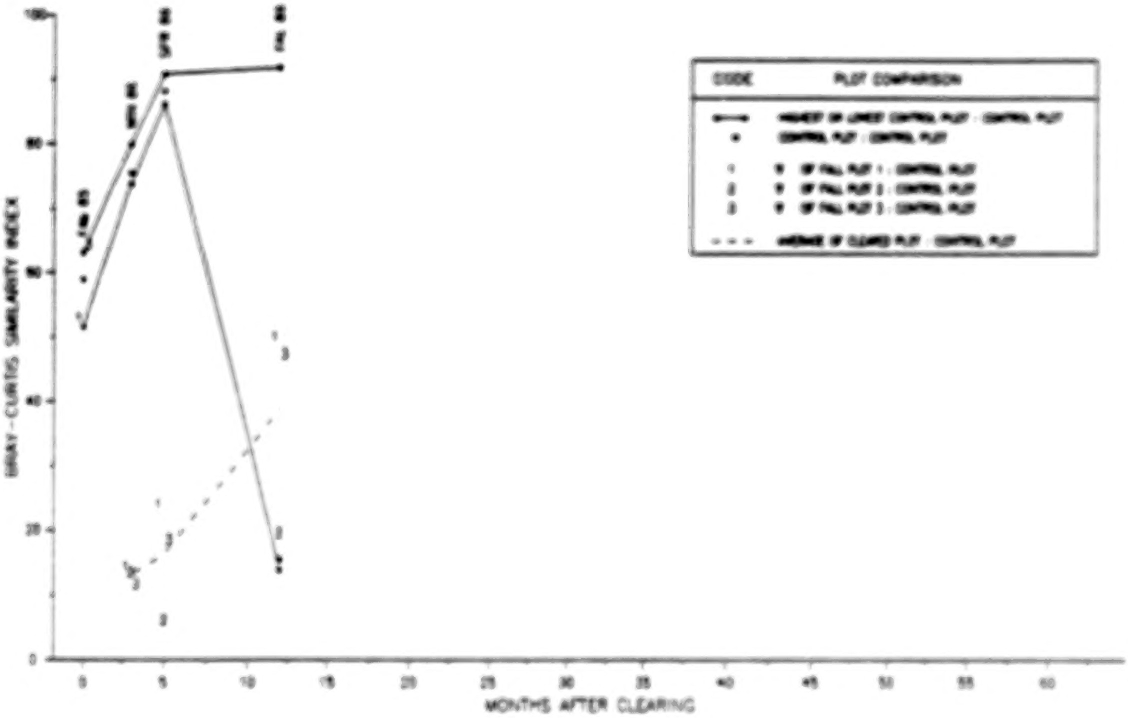


Figure I-37. *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Pt. Sierra Nevada (E).

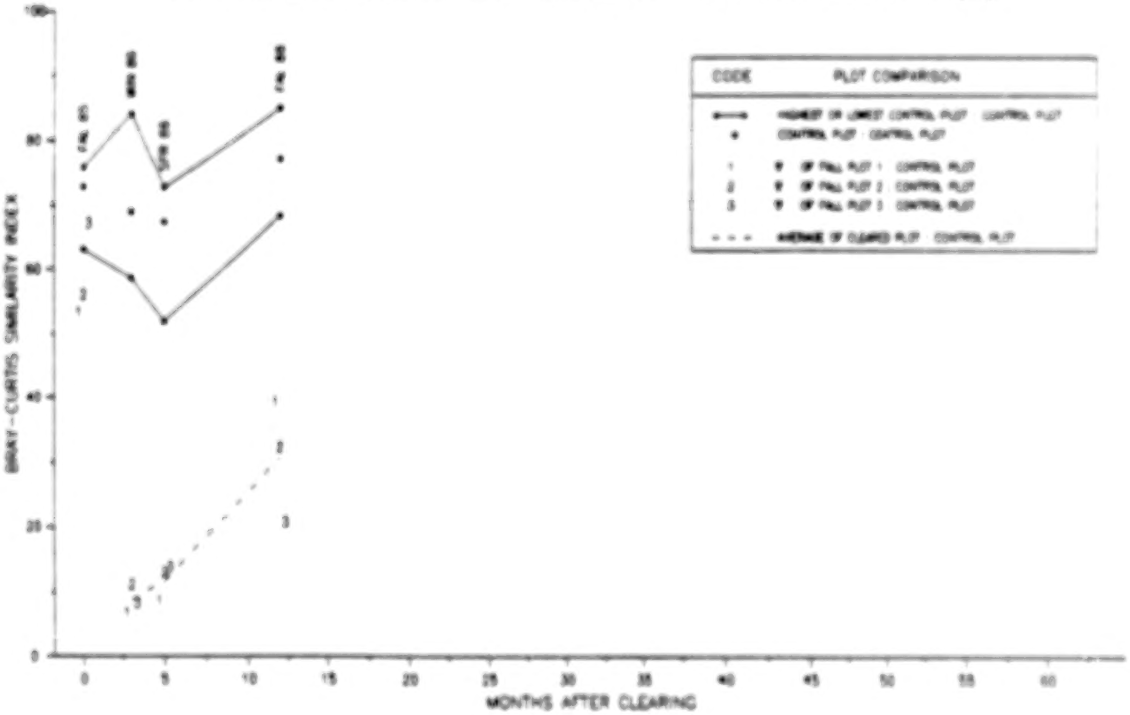


Figure I-38. *Endocladia/Mastocarpus papillatus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Diablo Canyon (F).

plots at other sites are within the range of control similarities. Recovery rates in the spring clearings appear to be inversely correlated with the abundance of ephemeral species and the species richness of a site. The similarities of both spring and fall clearings to control plots after 12 months of recovery time were nearly equal, suggesting seasonal differences in clearing have no obvious effects on recovery rate. Kibesillah Hill (A) is an exception as similarity to controls was much higher for the spring clearings after 12 months than for the fall clearings after 12 months (Figure I-21 vs. I-33). None of the data suggest recovery is correlated with latitude.

Mytilus Assemblage

Results

Spring Clearings. Eighteen months after clearing, the total number of taxa found during succession in the spring clearings ranged from 35 [Kibesillah Hill (A) and Bolinas (C)] to 56 [Pescadero Rocks (D)] (Table I-13). The number of taxa per site was generally higher than in the spring clearings in the *Endocladia/Mastocarpus papillatus* assemblage. Variation in richness does not correlate with the latitudinal gradient of the sites, and the correlation with the richness of the control plots (Table I-6) is not significant (correlation coefficient, $r = 0.600$, $p>0.2$).

Qualitative observations in the *Mytilus* assemblage through fall 1986 indicate mussel recruitment in the cleared plots has occurred but has been patchy and at low densities. Mussels were noted only five times until spring 1986; only twice were the mussels thought to be recruits. The most observations of recruits were made in spring 1986 at Pescadero Rocks and Sea Ranch. However, by fall 1986, observations of recruits at these sites dropped. At other sites, only a few (1-3) patchily distributed recruits have been noted. Occasionally, larger mussels have also been observed, sometimes in cracks or pools.

There is no apparent relationship between recruitment patterns in the *Endocladia* assemblage and recruitment in the *Mytilus* assemblage. In the *Endocladia* assemblage, mussel recruitment was noted at four sites: Point Sierra Nevada (E), Pescadero Rocks (D), Bolinas (C), and Sea Ranch (B). Few to many recruits have been noted in both control and cleared plots. Recruits were noted at Pescadero Rocks (D) during every sampling period but only during two or three sampling periods at other sites.

In contrast to the spring clearings in the *Endocladia/Mastocarpus papillatus* assemblage, all sites except Kibesillah Hill (A) had a high number of abundant (cover) taxa, and all sites except Bolinas (C) had an initially high cover of ephemeral algal taxa (Figures I-39 - I-44). These ephemerals declined dramatically within 12 months at most sites, leaving bare rock or rock beneath an overstory as the most abundant "taxon". This was true at all sites except Pescadero Rocks (D) where perennial algae (crustose corallines, *Bossiella plumosa*, and *Iridaea flaccida*) had the highest cover after 18 months (Figure I-42).

Limpets were extremely abundant in the spring clearings at all sites (Table I-14). They increased in abundance with time at two southern sites [Diablo Canyon (F), Pescadero Rocks (D)], but increased through spring 1986 and then decreased at the other sites [Point Sierra Nevada (E), Bolinas (C), Sea Ranch (B), Kibesillah Hill (A)].

Littorina scutulata/plena was abundant at Bolinas (C) and Kibesillah Hill (A). Surprisingly, this grazer was not abundant at Point Sierra Nevada (E) where it was

Table I-13. Taxa Sampled in the *Mytilus* Assemblage Spring-Cleared Plots, Summer 1985 - Fall 1986.

SITE:	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
SPECIES						
Acanthina sp(p).			X			
Acanthina spirata			X			
Alaria marginata				X		X
Amphipoda, unident.	X	X	X	X	X	X
Amphissa columbiana	X					
Amphissa versicolor	X					
Analipus japonicus	X	X	X	X	X	X
Anthopleura elegantissima	X		X			X
Balanus glandula	X	X	X	X	X	X
Binghamia sp(p).				X		
Bossiella plumosa	X	X		X	X	X
Brown blades				X		
Brown crusts		X			X	
Calliarthron tuberculosum						X
Callithamnion pikeanum					X	
Callophyllis heanophylla		X				
Ceramium eatonianum			X			
Chaetomorpha linum		X		X	X	
Chrysophyta, unident.		X		X	X	X
Chthamalus sp(p).	X	X	X	X	X	X
Cirratulidae, unident.		X			X	
Cladophora columbiana	X	X	X	X	X	X
Cladophora sp(p).					X	X
Cladophora stimpsonii				X		
"Collisella" scabra	X	X	X	X	X	X
Colpomenia sinuosa				X		X
Copepoda, unident.				X	X	X
Corallina officinalis		X		X	X	
Corallina vancouveriensis	X	X		X	X	X
Cottidae, unident.	X	X				
Crustose corallines, unident.	X	X	X	X	X	X
Cryptosiphonia woodii	X		X	X		
Cylindrocarpus rugosus			X	X	X	X
Diodora aspera						X
Diptera-Diptera larvae	X	X	X	X	X	X
Egregia menziesii				X	X	X
Endocladia muricata	X	X	X		X	X
Enteromorpha intestinalis		X				
Enteromorpha linza		X		X		X
Enteromorpha sp(p).		X		X		
Fissurella volcano				X		X
Fucus distichus	X	X	X			
G.A.T.G.O.R.	X	X		X		X

Table I-13. (Continued)

SITE:	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
SPECIES						
Gastropoda egg cases			X			
Gelidium coulteri			X		X	
Gigartina canaliculata	X					
Green blades				X		
Green filaments					X	
Haliotis rufescens						X
Halosaccion glandiforme	X	X				
Hemigrapsus nudus			X			
Insecta, unident.		X				
Iridaea cordata		X	X	X		
Iridaea flaccida	X	X	X	X	X	X
Iridaea heterocarpa	X	X	X	X		
Iridaea sp(p).		X		X		
Isopoda, unident.	X	X	X		X	X
Katharina tunicata					X	
Lacuna sp(p).		X				X
Leathesia difformis		X				
Lepidochitona dentiens	X	X	X	X		X
Lepidochitona hartwegii	X			X	X	
Leptasterias sp(p).	X	X		X		X
Leptoplanidae, unident.		X				
Littorina keenae	X				X	X
Littorina scutulata/plena	X	X	X	X	X	X
Lomentaria sp(p).				X		
Lottia asmi	X		X			X
Lottia digitalis	X	X	X	X	X	X
Lottia gigantea		X		X	X	X
Lottia limatula	X	X		X	X	X
Lottia paradigitalis	X	X	X	X	X	X
Lottia pelta	X	X	X	X	X	X
Lottia sp(p).	X	X	X	X	X	X
Margarites sp(p).		X				
Mastocarpus jardinii				X		
Mastocarpus papillatus	X	X	X	X	X	X
Microcladia borealis	X	X		X	X	X
Mopalia muscosa	X	X	X		X	
Mytilus californianus	X	X	X	X	X	X
Mytilus edulis	X					
Nemertea, unident.		X	X	X	X	X
Neorhodomela larix		X				
Neorhodomela oregona	X		X			
Nereidae, unident.				X		X
Nucella emarginata	X	X	X		X	
Nucella lamellosa		X				

Table I-13. (Continued)

SITE:	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
SPECIES						
Nuttallina californica	X	X	X	X	X	X
Ocenebra circumtexta	X	X	X		X	
Odonthalia floccosa	X	X	X			
Odonthalia washingtoniensis		X				
Pachygrapsus crassipes		X	X	X		X
Pagurus sp(p).	X	X	X			
Pelvetia-Pelvetiopsis sp(p).	X		X	X		
Petalonia fascia		X		X		X
Petrocelis sp(p).	X	X	X	X	X	X
Petrolisthes cinctipes		X				
Phaeostrophion irregulare					X	
Phidiana crassicornis	X					
Phragmatopoma californica	X		X		X	X
Plocamium sp(p).			X			
Plocamium violaceum		X		X		
Pollicipes polymerus		X		X	X	X
Polychaeta, unident.	X	X	X	X	X	X
Polyplacophora, unident.		X				
Polysiphonia hendryi	X	X	X	X	X	X
Polysiphonia nathaniellii					X	X
Polysiphonia sp(p).	X				X	X
Porphyra lanceolata				X		X
Porphyra perforata			X		X	X
Porphyra sp(p).		X		X	X	
Prionitis lanceolata				X		
Prionitis lyallii				X		
Pterocladia caloglossoides				X		
Pterosiphonia bipinnata			X			
Pterosiphonia dendroidea			X			
Pterosiphonia pennata		X				
Pugettia producta						X
Pugettia sp(p).						X
Ralfsia sp(p).	X	X	X	X	X	X
Red blades		X		X	X	
Red crusts	X	X		X	X	
Red filaments		X	X	X		
Rhodoglossum affine				X	X	
Scytosiphon dotyi					X	
Scytosiphon lomentaria				X	X	X
Semibalanus cariosus	X	X		X		
Spirorbidae, unident.		X				
Spongomorpha mertensii		X				
Strongylocentrotus purpuratus		X		X	X	X
Tectura scutum	X	X			X	X

Table I-13. (Continued)

SITE:	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
SPECIES						
Tegula brunnea			X	X		
Tegula funebralis	X	X	X	X	X	X
Terebellidae, unident.		X				
Tetraclita rubescens	X			X		X
Tonicella lineata	X			X		
Ulva californica		X		X	X	X
Ulva lobata				X	X	X
Ulva sp(p).				X		X
Urospora doliifera						X
Urospora penicilliformis	X	X				X
TOTAL TAXA	61	79	55	77	63	69

KH = Kibesillah Hill, SR = Sea Ranch, B = Bolinas, PR = Pescadero Rocks, PSN = Pt. Sierra Nevada, DC = Diablo Canyon. (A-F) designate latitudinal order (A = most northern, F = most southern site).

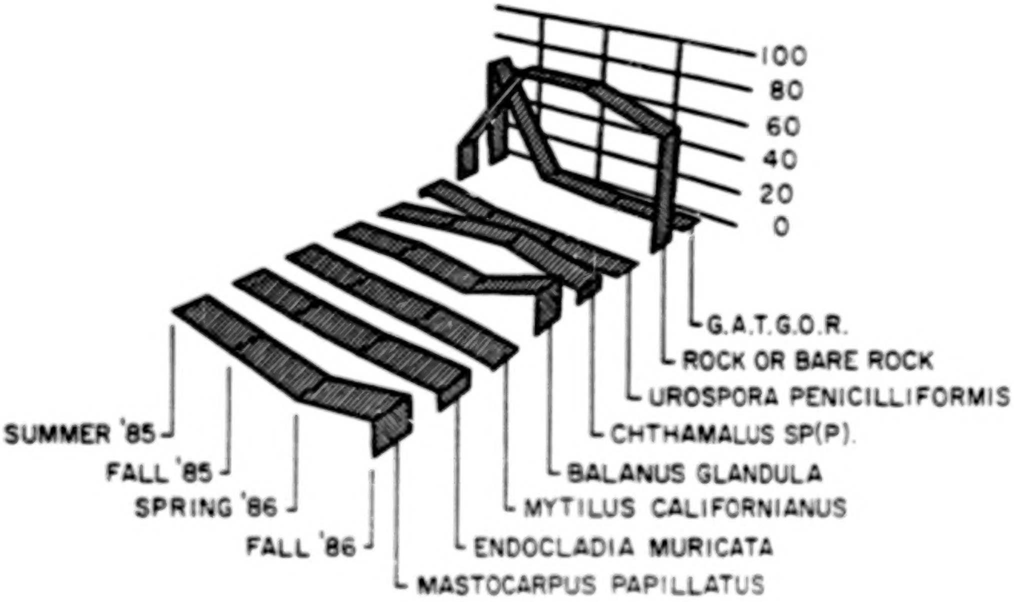


Figure I-39. *Mytilus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Kibesillah Hill (A).

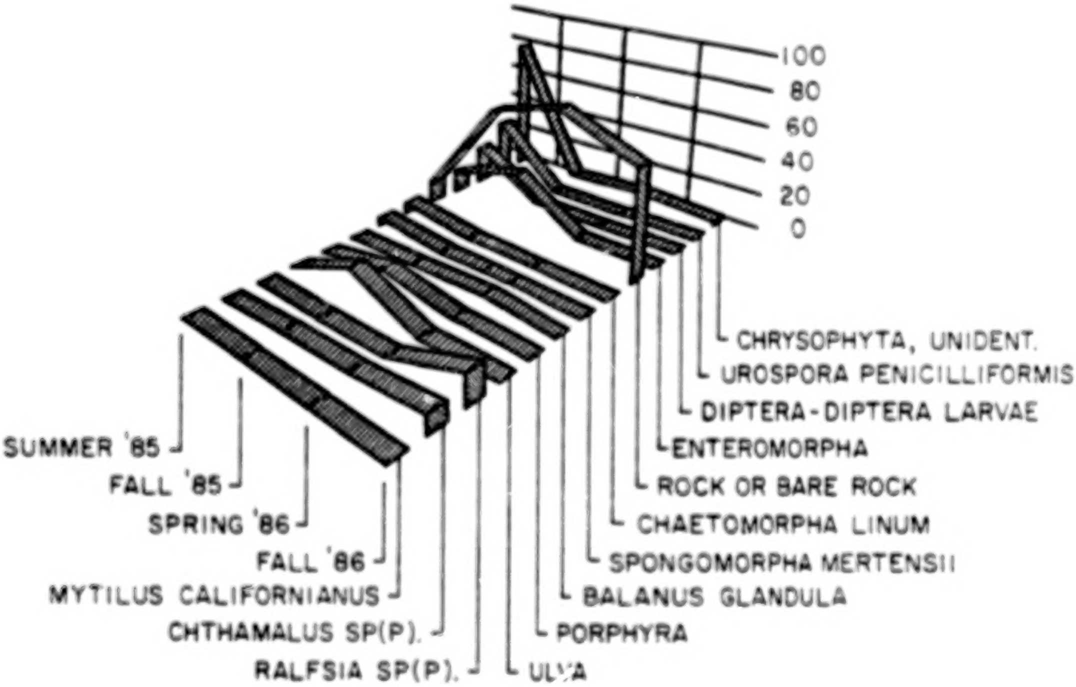


Figure I-40. *Mytilus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Sea Ranch (B).

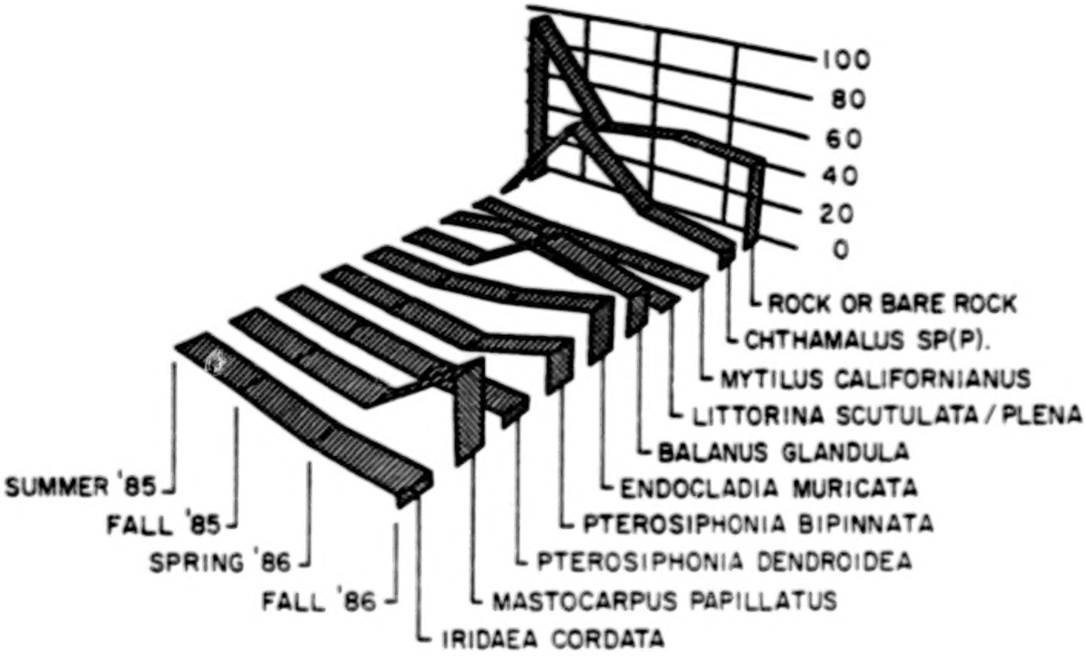


Figure I-41. *Mytilus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Bolinas (C).

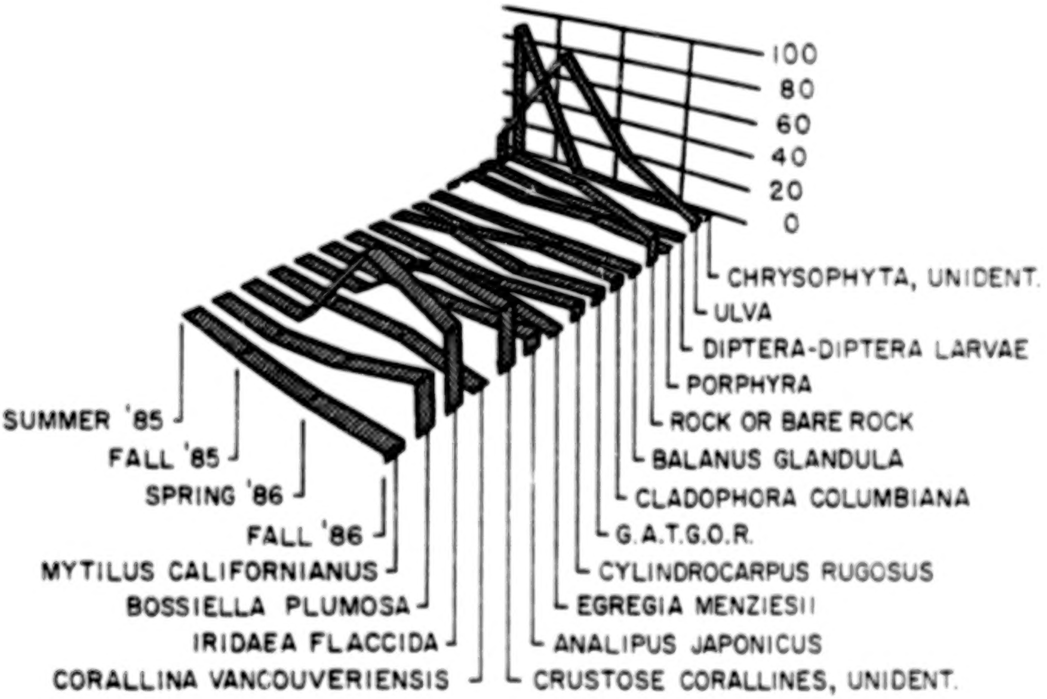


Figure I-42. *Mytilus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Pescadero Rocks (D).

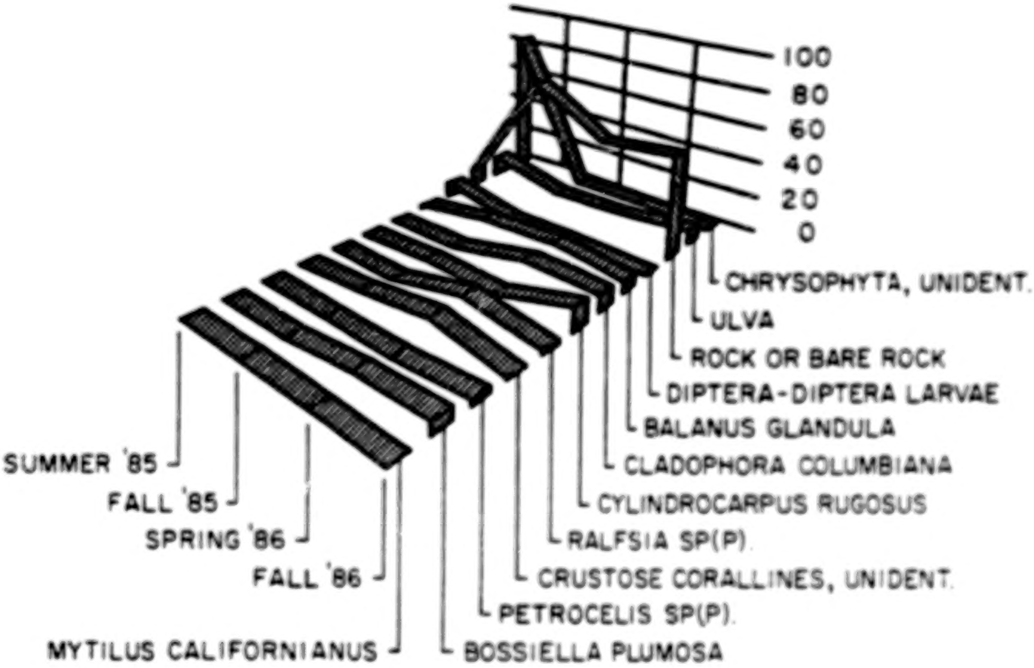


Figure I-43. *Mytilus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Pt. Sierra Nevada (E).

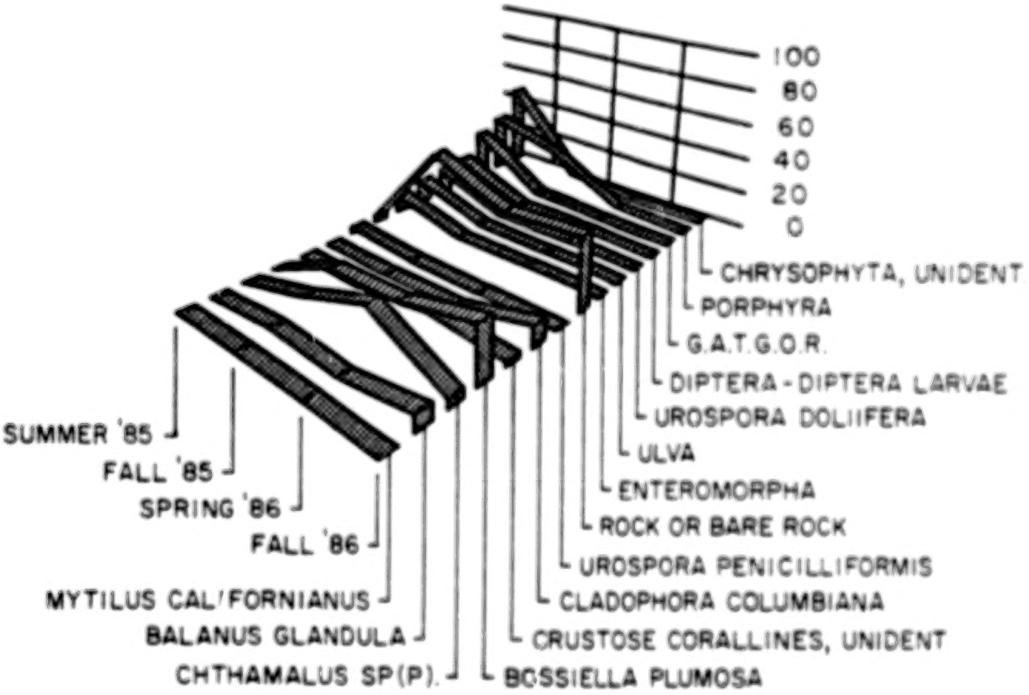


Figure I-44. *Mytilus* Assemblage: Temporal Abundance Data for Spring-Cleared Plots (Mean of 3 Plots) - Diablo Canyon (F).

Table I-14. Abundance (Counts) of the Dominant Motile Species in the *Mytilus* Assemblage Spring-cleared Plots, Summer 1985 - Fall 1986. Mean* (Standard Deviation).

Name	Sampling Period	Kibesillah Hill (A)		Sea Ranch (B)		Bolinas (C)		Pescadero Rocks (D)		Pt. Sierra Nevada (E)		Diablo Canyon (F)	
CHITONS													
	Summer 85	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	1.33	(1.53)
	Fall 85	1.33	(2.31)	1.00	(1.73)	0.00	(0.00)	2.67	(2.89)	3.00	(1.73)	12.67	(3.21)
	Spring 86	0.00	(0.00)	2.08	(3.61)	0.33	(0.58)	5.33	(3.06)	4.00	(2.65)	7.67	(0.58)
	Fall 86	0.33	(0.58)	0.33	(0.58)	0.33	(0.58)	6.00	(6.08)	5.67	(3.51)	4.33	(3.06)
GRAZER LIMPETS													
	Summer 85	7.67	(5.69)	21.42	(10.87)	12.00	(9.67)	2.33	(2.08)	12.33	(4.51)	24.17	(17.96)
	Fall 85	101.17	(43.48)	105.08	(70.51)	11.75	(7.38)	47.83	(44.16)	110.92	(106.11)	115.75	(54.58)
	Spring 86	328.08	(69.04)	748.25	(683.15)	154.25	(78.41)	52.17	(34.44)	593.67	(493.11)	222.50	(78.63)
	Fall 86	239.83	(35.29)	319.67	(120.20)	101.75	(24.56)	169.92	(40.23)	415.58	(209.94)	295.00	(63.73)
LITTORINA SCUTULATA/PLENA													
	Summer 85	22.58	(11.27)	0.67	(1.15)	13.08	(10.13)	3.08	(3.13)	7.00	(8.89)	1.00	(1.00)
	Fall 85	136.67	(56.01)	7.50	(7.76)	388.25	(170.77)	27.08	(25.26)	62.42	(62.25)	3.67	(6.35)
	Spring 86	211.33	(104.88)	2.33	(4.04)	214.33	(77.29)	7.50	(6.61)	39.92	(29.31)	3.75	(6.50)
	Fall 86	576.75	(182.39)	47.67	(50.06)	170.25	(138.90)	1.00	(1.00)	27.25	(25.68)	2.67	(4.62)
NUCELLA EMARGINATA													
	Summer 85	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 85	0.33	(0.58)	3.08	(4.50)	1.33	(0.58)	0.00	(0.00)	0.67	(0.58)	0.00	(0.00)
	Spring 86	1.33	(1.15)	3.00	(5.20)	0.67	(0.58)	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)
	Fall 86	2.00	(1.73)	5.33	(3.79)	8.33	(5.13)	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)
TEGULA BRUNNEA													
	Summer 85	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 85	0.00	(0.00)	0.00	(0.00)	5.33	(9.24)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Spring 86	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 86	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
TEGULA FUNEBRALIS													
	Summer 85	9.00	(7.94)	0.00	(0.00)	19.67	(6.51)	0.00	(0.00)	0.00	(0.00)	0.33	(0.58)
	Fall 85	27.42	(8.23)	0.33	(0.58)	7.67	(9.29)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Spring 86	9.33	(11.15)	3.00	(5.20)	2.67	(2.08)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 86	3.67	(2.52)	0.00	(0.00)	23.00	(4.58)	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)

*Mean number of individuals per 3 plots [value for each plot based on (sum of counts for 3 quadrats) #/0.1875 sq.m].

extremely abundant in the spring clearings in the *Endocladia/Mastocarpus papillatus* assemblage (Table I-10).

No spring-cleared plots in the *Mytilus* assemblage have recovered at any site. Average similarities of cleared plots to controls are around 20 percent, and there has been very little change in these values during the last three sampling periods (Figures I-45 - I-50). This seems to reflect the lack of mussel recruitment and the rapid colonization and persistence of most other taxa in the cleared plots.

Fall Clearings. After 12 months, the accumulated number of taxa per site in the fall-cleared plots varied between 29 [Bolinas (C)] and 46 [Pescadero Rocks (D); Table I-15]. The rank order of sites by number of taxa per site is very similar to that of the spring clearings in the *Mytilus* assemblage but, like the spring clearings, the species richness of the cleared plots was not significantly correlated with control plot richness (Table I-6, correlation coefficient $r = 0.612$, $p>0.2$). *Mytilus californianus* was not sampled in any fall clearings (Table I-15). It is included in the abundance-time graphs discussed below because it is characteristic of the assemblage.

The early taxonomic composition of abundant (cover) ephemeral algae was similar to that of the spring clearings, with diatoms, *Porphyra* sp(p)., and *Ulva* sp(p)., being most common (Figures I-51 - I-56). However, the abundance of these ephemeral algae was generally lower than in the spring clearings, and considerable portions of clearings at all sites remained unoccupied (rock or bare rock in Figures I-51 - I-56) throughout the 12 months of succession. There were also spring-fall differences in the species composition of longer-lived species, the most notable being for *Egregia menziesii*. This kelp did not occur in any of the spring clearings but has become abundant in the fall clearings at all southern sites (Figures I-54 - I-56). Other potential latitudinal differences in the colonization of particular species have not yet been assessed. It will be difficult to assess the possible impact of such latitudinal or site differences on recovery rate until a longer time series of data is available.

The most abundant motile taxa counted in the plots were limpets and *Littorina scutulata/plena* (Table I-16). The abundance of limpets was lower than in the spring-cleared plots for the same clearing age at four of the six sites (fall 1986 in Table I-16 vs. spring 1986 in Table I-14), but abundances were very much lower at Sea Ranch (B), Kibesillah Hill (A), and Point Sierra Nevada (E). As in the spring-cleared plots, *Littorina scutulata/plena* abundance was especially high at Bolinas (C) and Kibesillah Hill (A), and *Tegula funebralis* was abundant at Bolinas (C). No latitudinal patterns are apparent in these data.

The similarity of all fall clearings to control plots (Figures I-57 - I-62) is still very low (10 - 30 percent).

Summary

Colonization by mussels has been rare at all sites and has largely occurred from the immigration of adults into plots. Very little larval recruitment has been observed on the substrate or within the algae. No spring- or fall-cleared plots in the *Mytilus* assemblage at any sites have completely recovered, and similarities to controls remain at 10 - 30 percent. The similarity of the spring clearings to the controls has generally not increased over the last 12 months. Recovery rates in this assemblage have obviously been reduced by the lack of significant mussel recruitment.

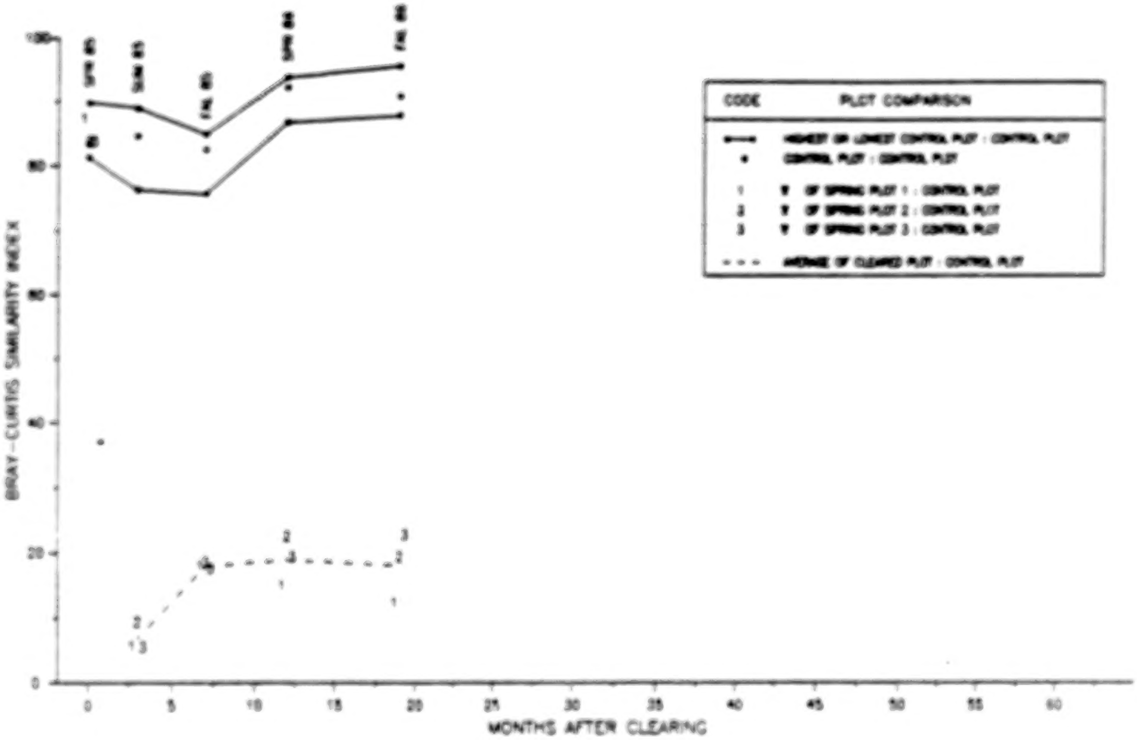


Figure I-45. *Mytilus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots - Kibesillah Hill (A).

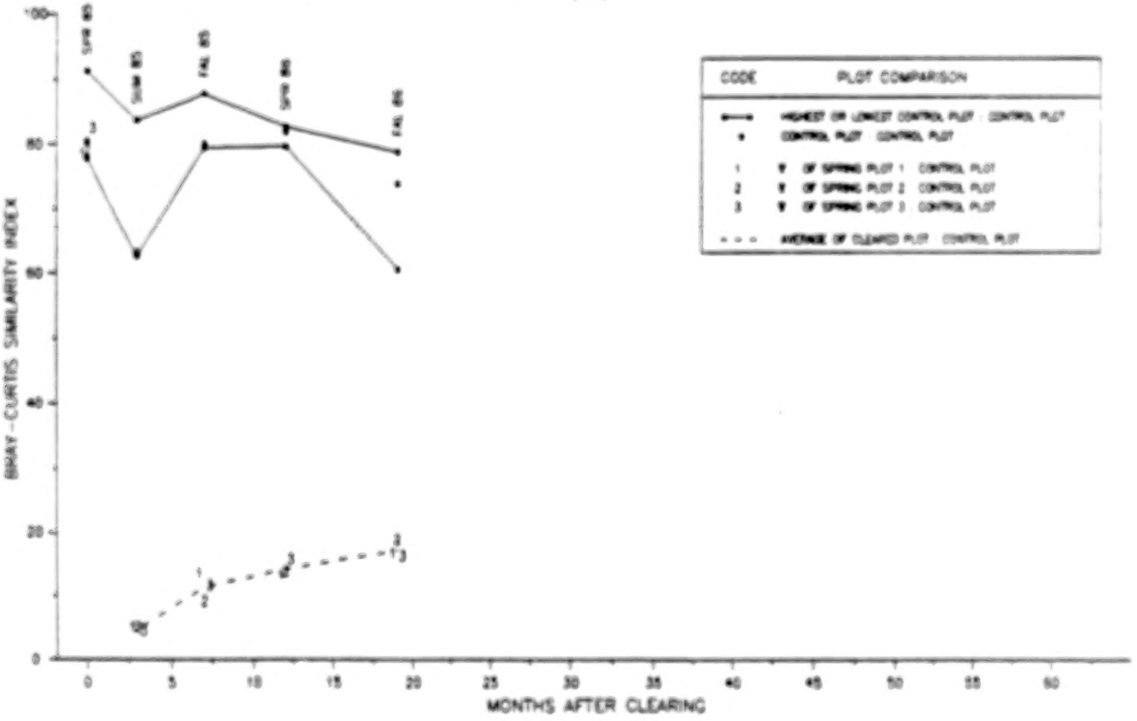


Figure I-46. *Mytilus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots - Sea Ranch (B).

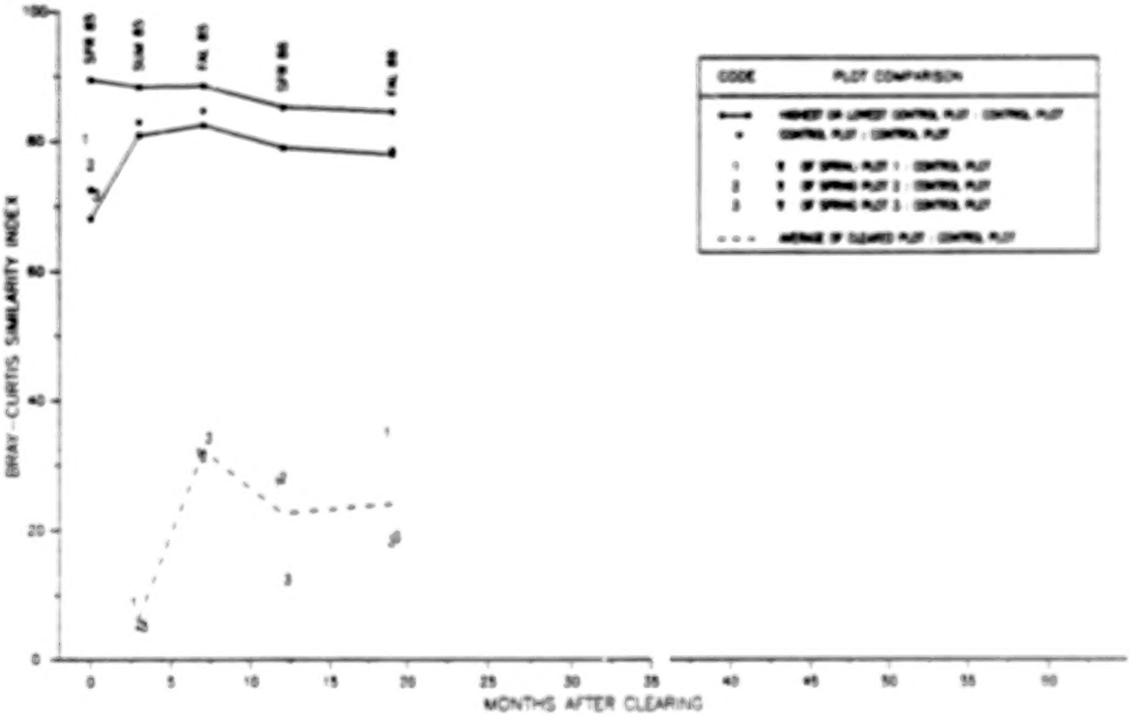


Figure I-47. *Mytilus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots - Bolinas (C).

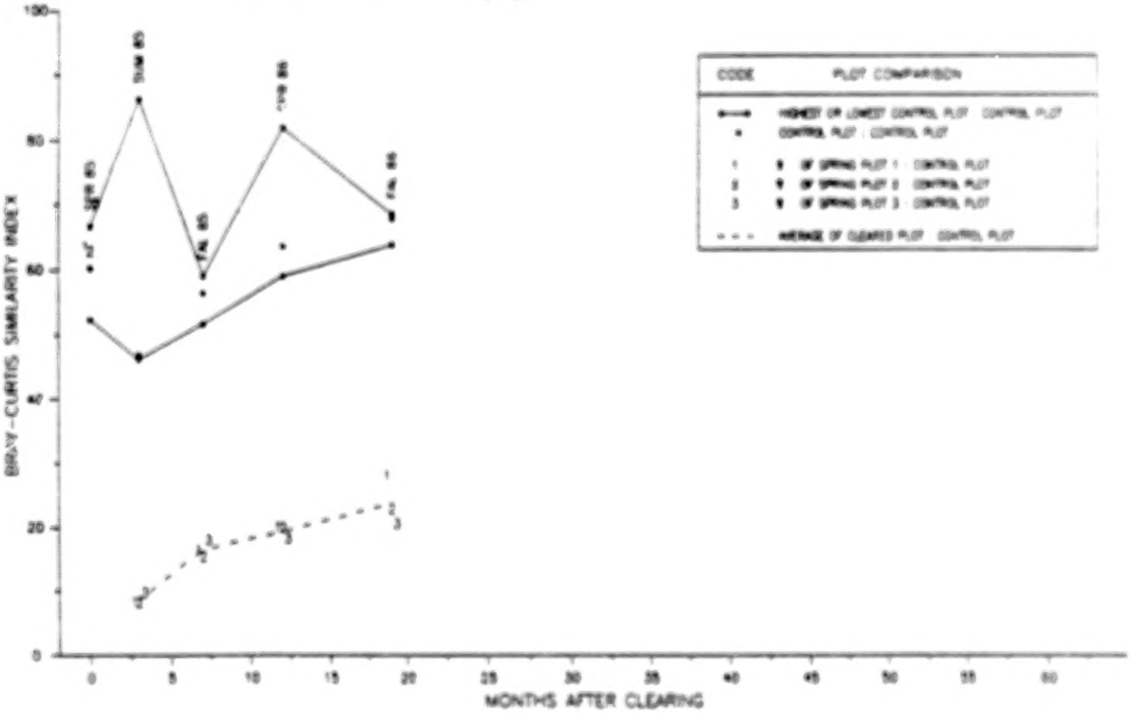


Figure I-48. *Mytilus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots - Pescadero Rocks (D).

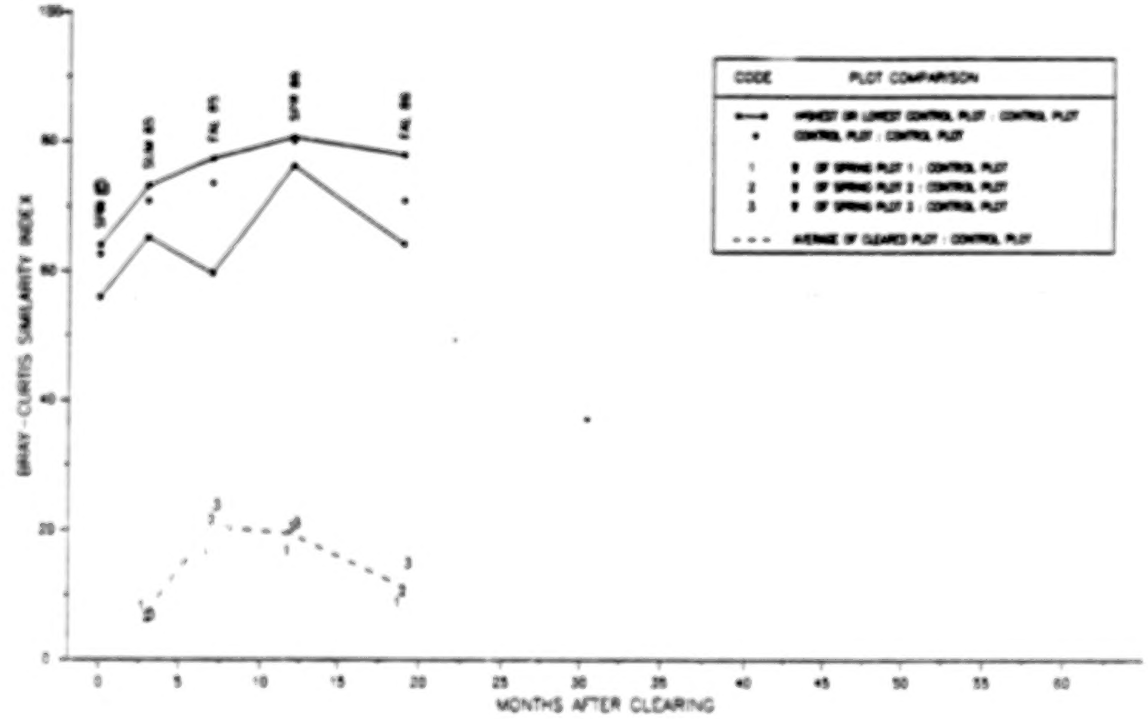


Figure I-49. *Mytilus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots - Pt. Sierra Nevada (E).

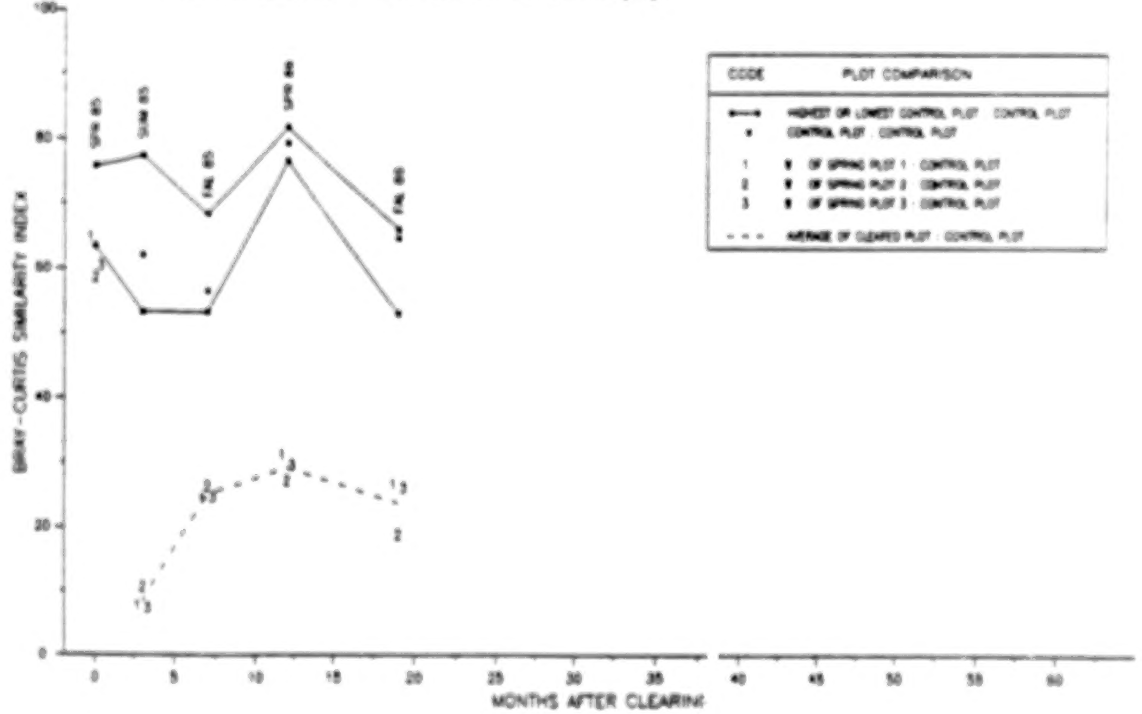


Figure I-50. *Mytilus* Assemblage: Bray Curtis Similarity between Spring-Cleared and Control Plots - Diablo Canyon (F).

Table I-15. Taxa Sampled in the *Mytilus* Assemblage Fall-Cleared Plots, Winter 1986 - Fall 1986.

SITE:	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
SPECIES						
Acmaea mitra				X		
Amphipoda, unident.		X	X	X	X	X
Analipus japonicus	X	X		X		
Anthopleura elegantissima			X			
Balanus glandula	X	X	X			X
Bangia fusco-purpurea		X	X			
Bossiella plumosa				X	X	X
Bossiella sp(p).						X
Brown blades			X			
Ceramium eatonianum				X		
Chrysophyta, unident.	X	X	X	X	X	X
Chthamalus sp(p).	X	X	X			X
Cladophora columbiana				X	X	X
Cladophora sp(p).						X
"Collisella" scabra	X	X	X	X	X	X
Colpomenia peregrina				X		
Colpomenia sinuosa	X					
Colpomenia sp(p).		X		X		
Copepoda, unident.			X	X		X
Corallina vancouveriensis	X					
Crustose corallines, unident.	X			X	X	X
Cylindrocarpus rugosus				X		
Diodora aspera				X		
Diptera-Diptera larvae	X	X	X	X	X	X
Egregia menziesii				X	X	X
Endocladia muricata				X		
Enteromorpha intestinalis	X			X		
Enteromorpha sp(p).				X		
Fissurella volcano						X
G.A.T.G.O.R.				X	X	X
Green blades		X				
Green filaments		X				
Haliotis cracherodii						X
Hemigrapsus nudus			X			
Insecta, unident.		X				
Iridaea cordata			X			
Iridaea flaccida	X	X	X	X		
Iridaea heterocarpa				X		
Iridaea sp(p).	X					
Isopoda, unident.			X		X	X
Lacuna sp(p).	X					
Lepidochitona dentiens		X			X	
Lepidochitona hartwegii	X					

Table I-15. (Continued)

SITE:	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
SPECIES						
Leptasterias sp(p).				X	X	X
Leptoplanidae, unident.		X				
Littorina scutulata/plena	X	X	X	X	X	
Lottia asmi	X	X	X			
Lottia digitalis	X	X	X	X	X	X
Lottia gigantea					X	X
Lottia limatula	X	X		X		X
Lottia ochracea						X
Lottia paradigitalis	X	X	X	X	X	X
Lottia pelta	X	X	X	X	X	X
Lottia sp(p).	X	X	X	X	X	X
Mastocarpus papillatus	X	X	X			
Mopalia muscosa	X	X			X	
Nemertea, unident.		X		X	X	X
Nucella emarginata	X	X	X		X	
Nuttallina californica	X	X		X	X	X
Ocenebra circumtexta					X	
Pachygrapsus crassipes			X		X	X
Pagurus sp(p).	X		X			
Pelvetia-Pelvetiopsis sp(p).					X	
Petalonia fascia		X		X		
Petrocelis sp(p).			X		X	X
Phaeostrophion irregulare	X			X		
Plocamium violaceum						X
Pollicipes polymerus				X		X
Polychaeta, unident.					X	
Polysiphonia hendryi	X	X			X	X
Porphyra lanceolata	X	X	X	X	X	X
Porphyra perforata	X	X		X		X
Porphyra sp(p).		X	X	X	X	X
Pugettia producta				X		
Ralfsia sp(p).	X	X	X	X		X
Red crusts	X				X	
Red filaments				X	X	X
Rhodoglossum affine				X		
Scytosiphon dotyi	X					
Scytosiphon lomentaria		X			X	
Strongylocentrotus purpuratus				X	X	X
Tectura scutum		X		X		X
Tegula funebralis	X	X	X		X	X

Table I-15. (Continued)

SITE:	KH (A)	SR (B)	B (C)	PR (D)	PSN (E)	DC (F)
SPECIES						
Ulva californica		X		X	X	X
Ulva lobata		X		X	X	X
Ulva sp(p).		X		X	X	X
Urospora wormskioldii		X				
TOTAL TAXA	34	40	29	46	38	43

KH = Kibesillah Hill, SR = Sea Ranch, B = Bolinas, PR = Pescadero Rocks, PSN = Pt. Sierra Nevada, DC = Diablo Canyon. (A-F) designate latitudinal order (A = most northern, F = most southern site).

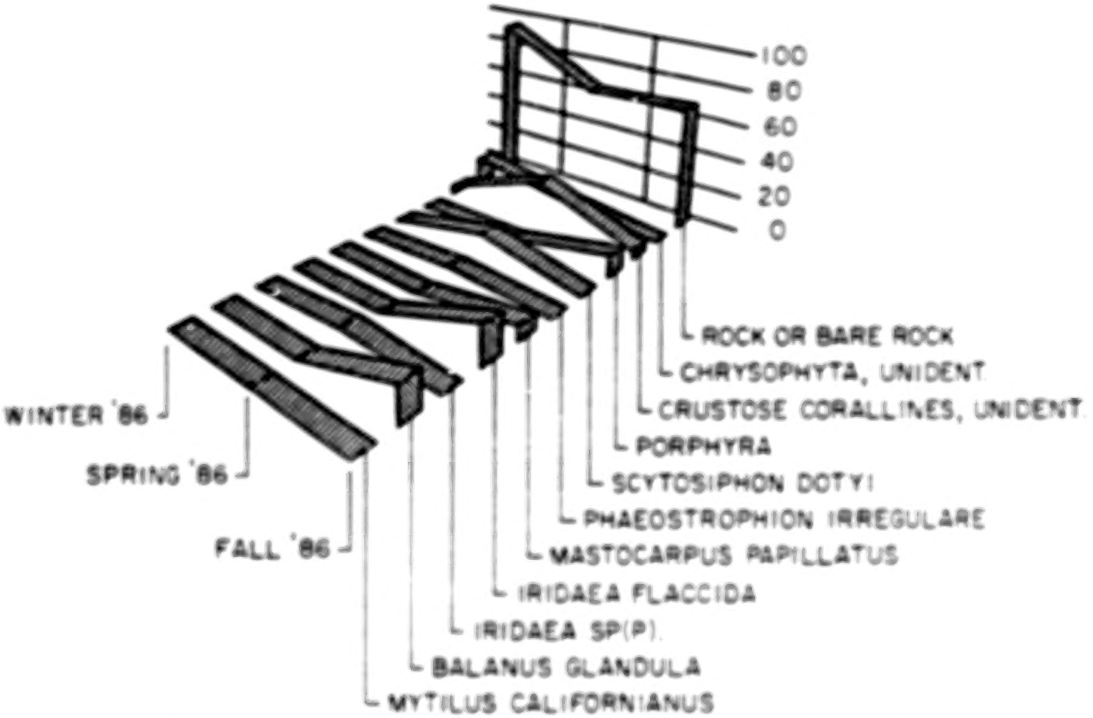


Figure I-51. *Mytilus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Kibesillah Hill (A).

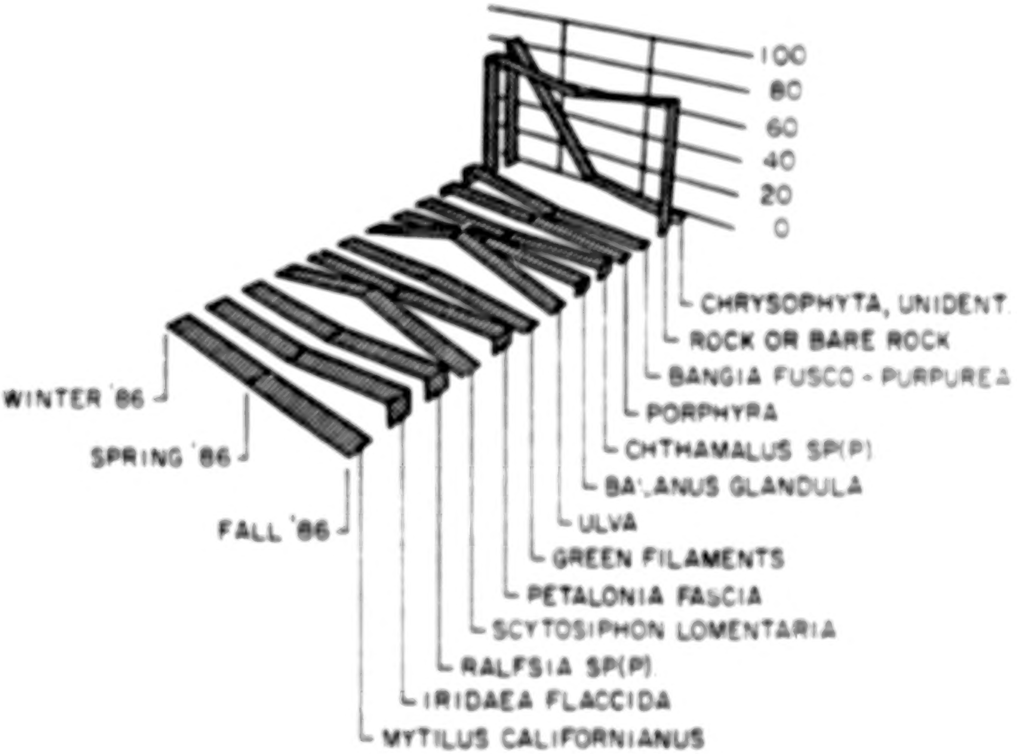


Figure I-52. *Mytilus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Sea Ranch (B).

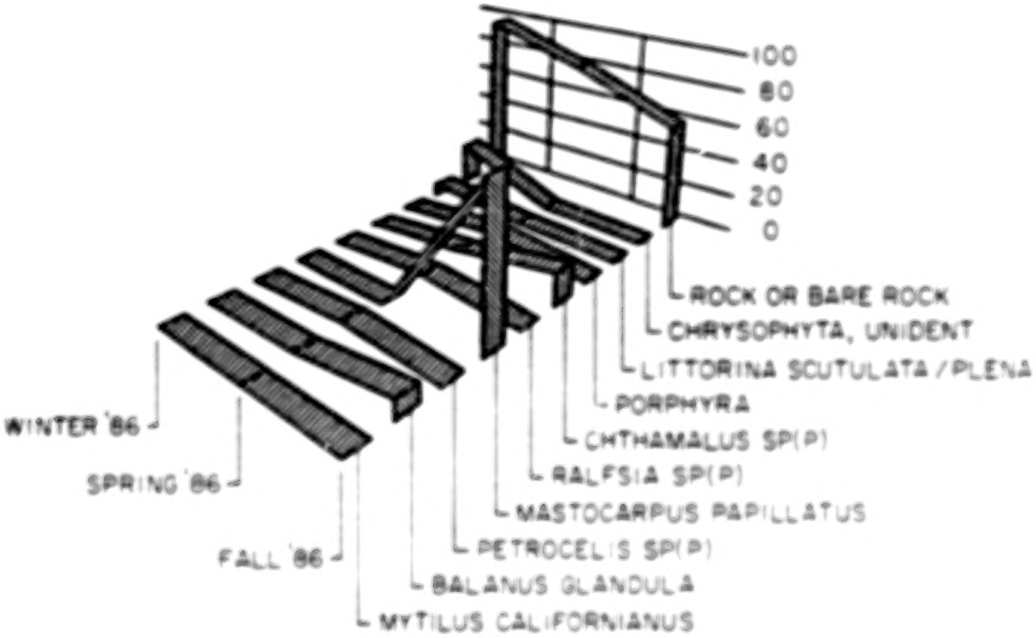


Figure I-53. *Mytilus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Bolinas (C).

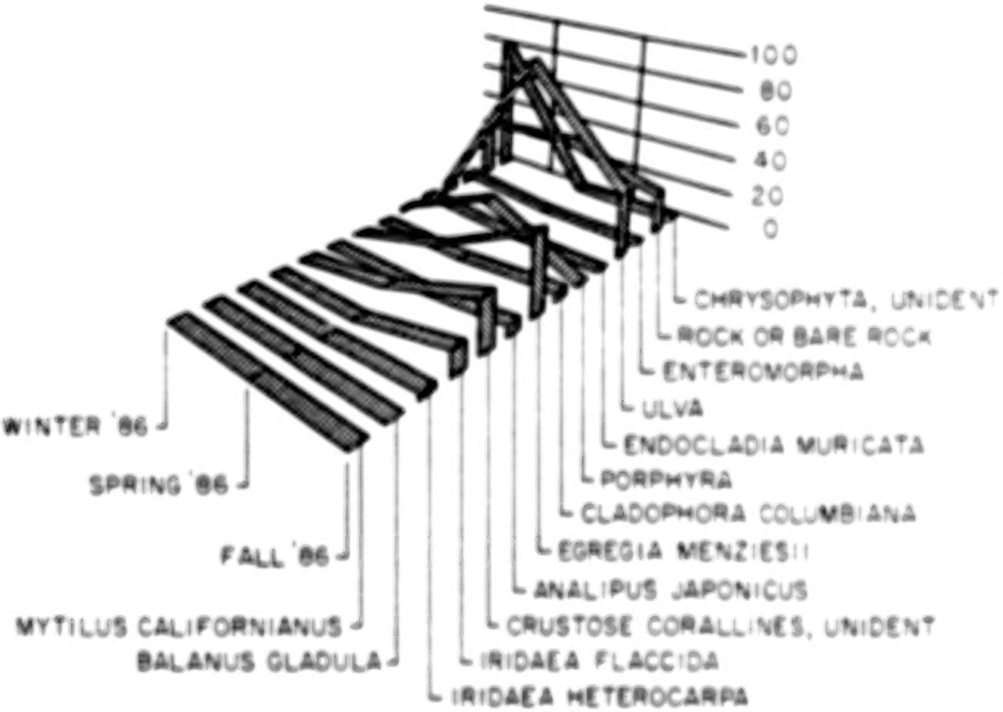


Figure I-54. *Mytilus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Pescadero Rocks (D).

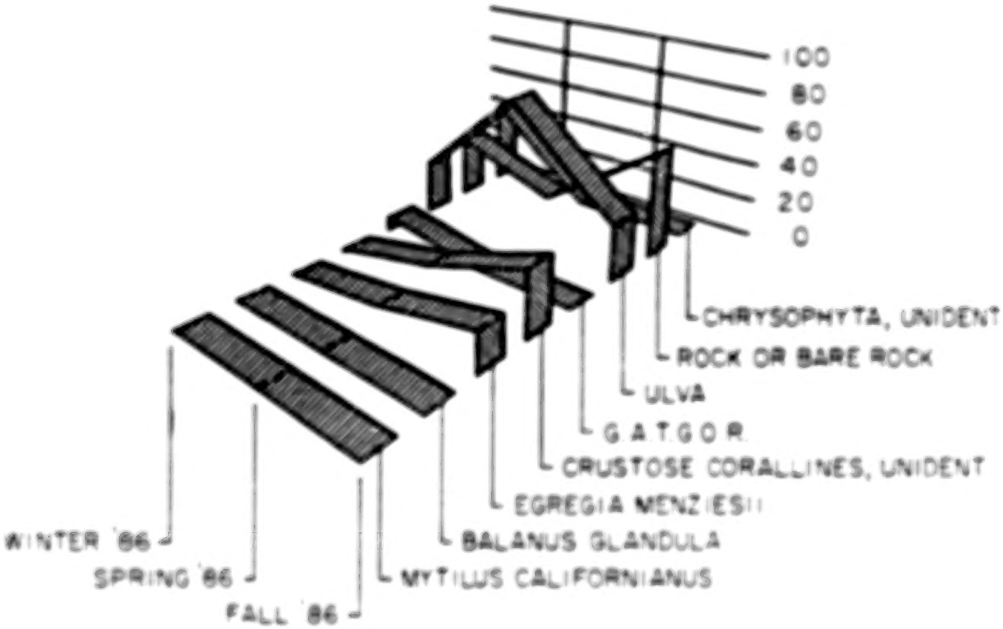


Figure I-55. *Mytilus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Pt. Sierra Nevada (E).

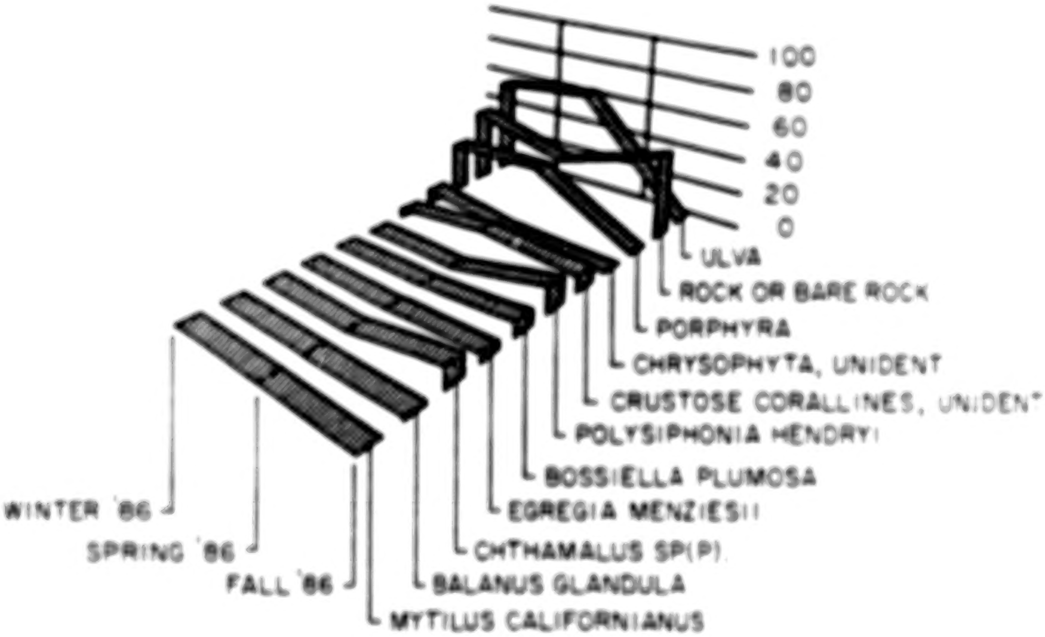


Figure I-56. *Mytilus* Assemblage: Temporal Abundance Data for Fall-Cleared Plots (Mean of 3 Plots) - Diablo Canyon (F).

Table I-16. Abundance (Counts) of the Dominant Motile Species in the *Mytilus* Assemblage Fall-cleared Plots, Winter 1986 - Fall 1986. Mean* (Standard Deviation).

Name	Sampling Period	Kibesillah Hill (A)		Sea Ranch (B)		Bolinas (C)		Pescadero Rocks (D)		Pt. Sierra Nevada (E)		Diablo Canyon (F)	
CHITONS													
	Winter 86	1.33	(1.53)	0.00	(0.00)	0.00	(0.00)	0.67	(1.15)	2.00	(2.00)	0.67	(0.58)
	Spring 86	1.33	(1.53)	0.33	(0.58)	0.00	(0.00)	0.00	(0.00)	1.67	(2.89)	0.33	(0.58)
	Fall 86	0.33	(0.58)	0.67	(0.58)	0.00	(0.00)	3.33	(3.06)	7.00	(2.65)	5.00	(2.00)
GRAZER LIMPETS													
	Winter 86	55.58	(55.59)	6.33	(3.06)	0.67	(1.15)	1.67	(1.53)	17.17	(15.67)	14.92	(7.44)
	Spring 86	69.67	(48.55)	48.00	(44.69)	3.42	(4.30)	1.67	(2.08)	153.42	(220.30)	51.00	(27.44)
	Fall 86	167.50	(110.54)	275.08	(124.93)	32.75	(5.02)	57.00	(17.58)	351.25	(298.51)	268.00	(180.57)
LACUNA SP(P).													
	Winter 86	6.25	(10.83)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Spring 86	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 86	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
LITTORINA SCUTULATA/PLENA													
	Winter 86	17.75	(5.58)	1.00	(1.73)	95.92	(16.63)	0.00	(0.00)	4.67	(8.08)	0.00	(0.00)
	Spring 86	55.42	(51.60)	2.42	(3.36)	94.50	(49.04)	0.00	(0.00)	1.67	(2.89)	0.00	(0.00)
	Fall 86	130.17	(43.32)	9.83	(9.63)	82.50	(51.67)	2.08	(3.61)	41.17	(71.30)	0.00	(0.00)
NUCELLA EMARGINATA													
	Winter 86	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)	0.00	(0.00)	0.33	(0.58)	0.00	(0.00)
	Spring 86	0.67	(1.15)	0.33	(0.58)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 86	2.67	(2.89)	2.00	(1.00)	6.00	(4.36)	0.00	(0.00)	1.67	(1.53)	0.00	(0.00)
TEGULA FUNEBRALIS													
	Winter 86	6.00	(3.00)	0.00	(0.00)	12.67	(2.31)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Spring 86	10.00	(5.57)	1.00	(1.73)	4.67	(3.21)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
	Fall 86	7.67	(8.02)	0.00	(0.00)	41.33	(28.71)	0.00	(0.00)	0.33	(0.58)	0.33	(0.58)

*Mean number of individuals per 3 plots [value for each plot based on (sum of counts for 3 quadrats) ÷ 0.1875 sq.m]

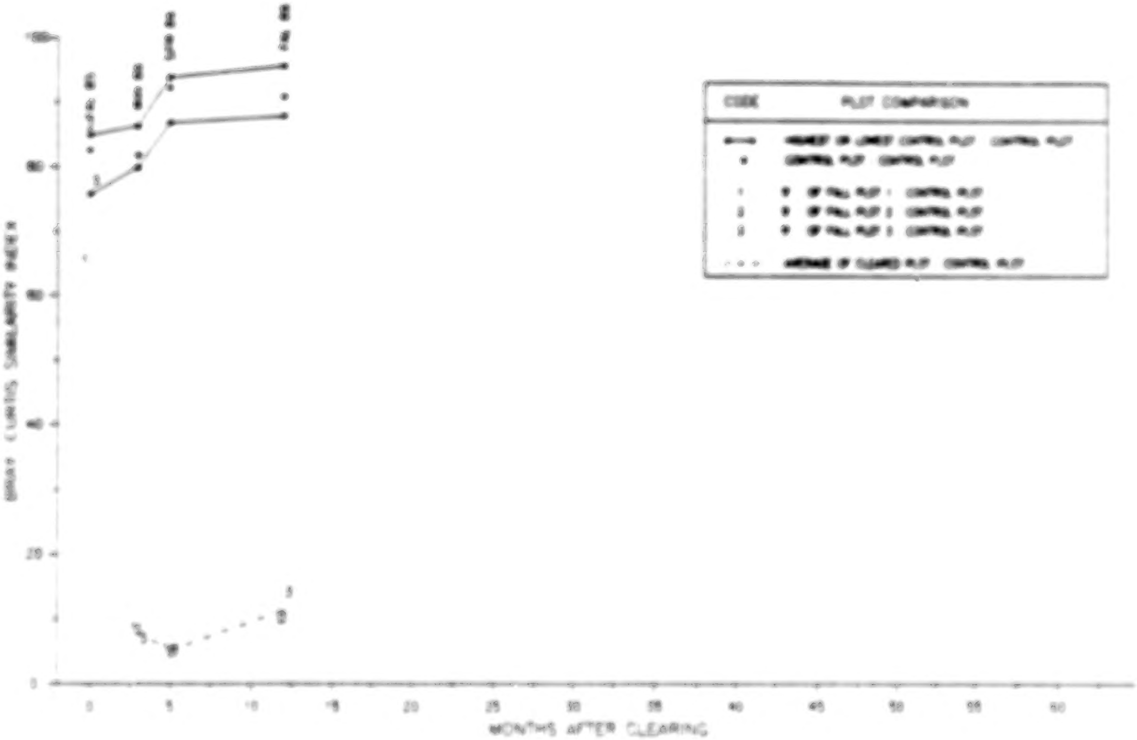


Figure I-57. *Mytilus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Kibesillah Hill (A).

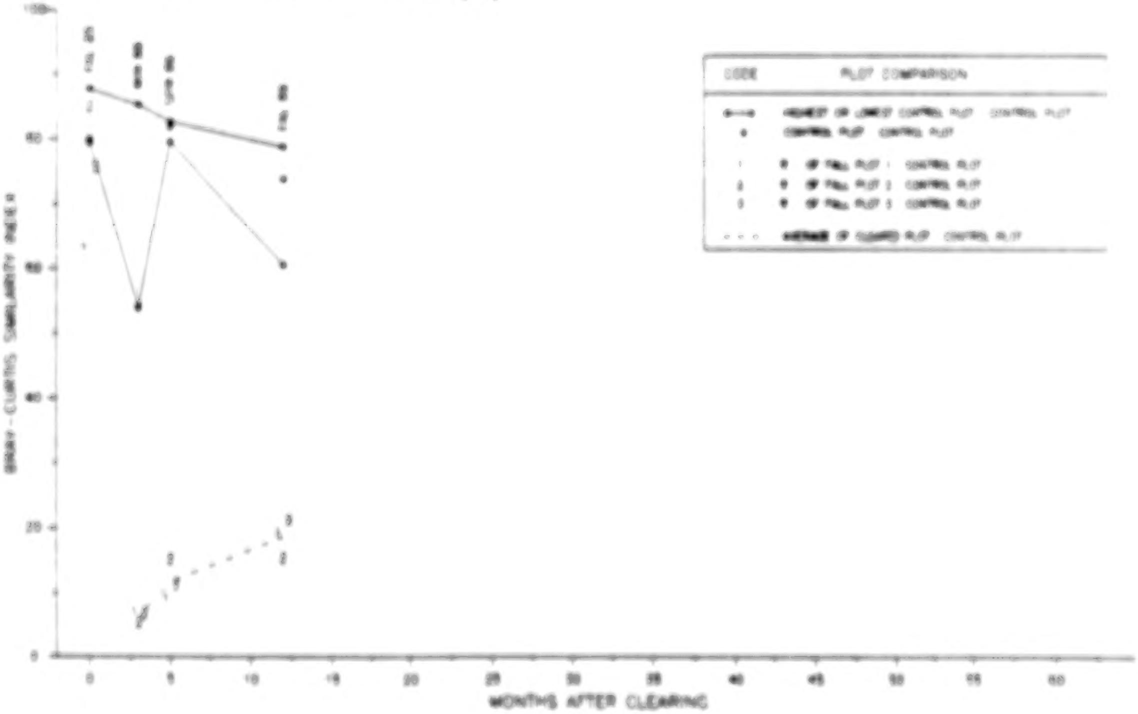


Figure I-58. *Mytilus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Sea Ranch (B).

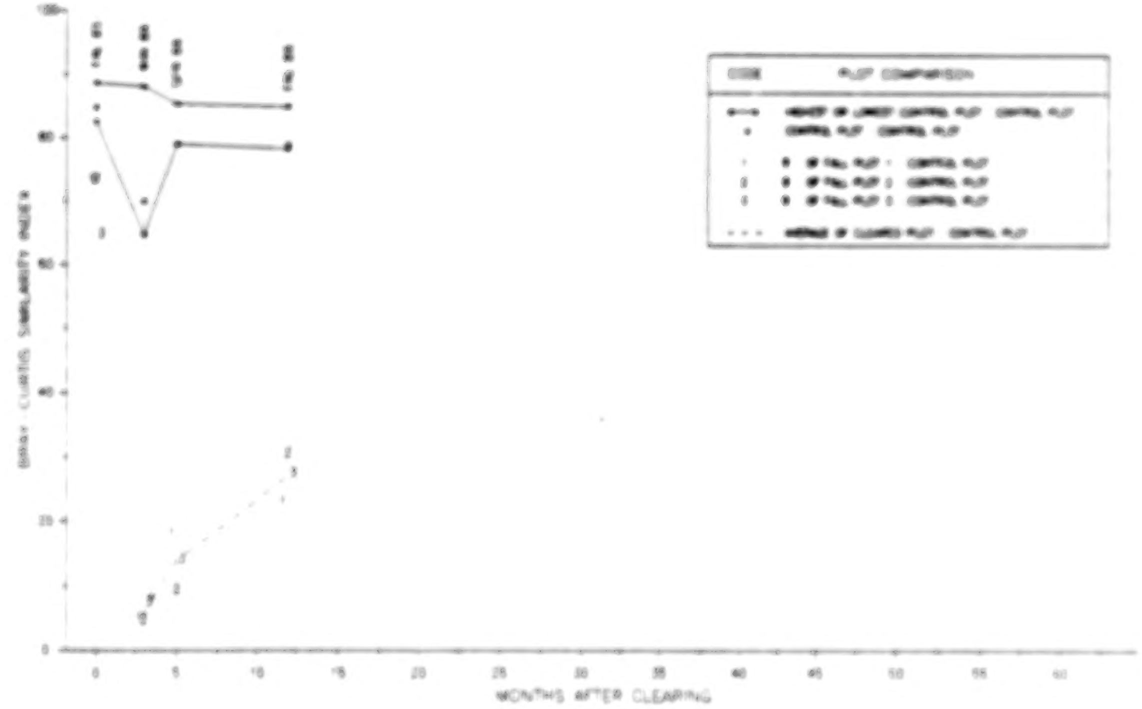


Figure 1-59. *Mytilus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Bolinas (C).

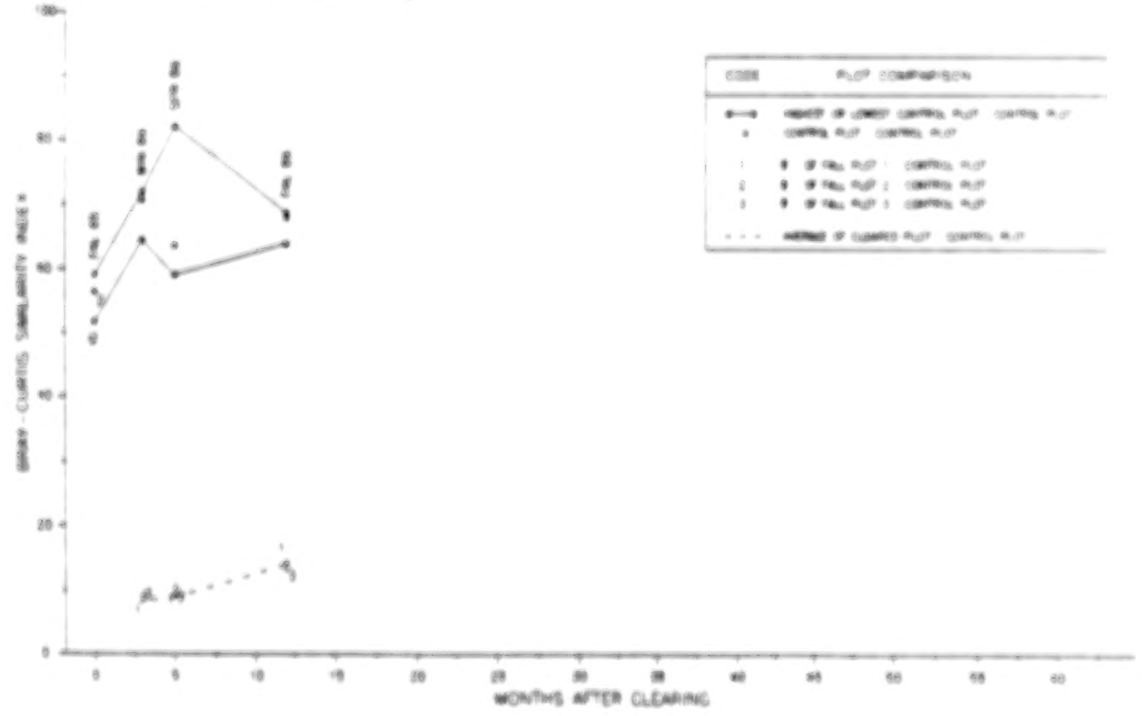


Figure 1-60. *Mytilus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Pescadero Rocks (D).

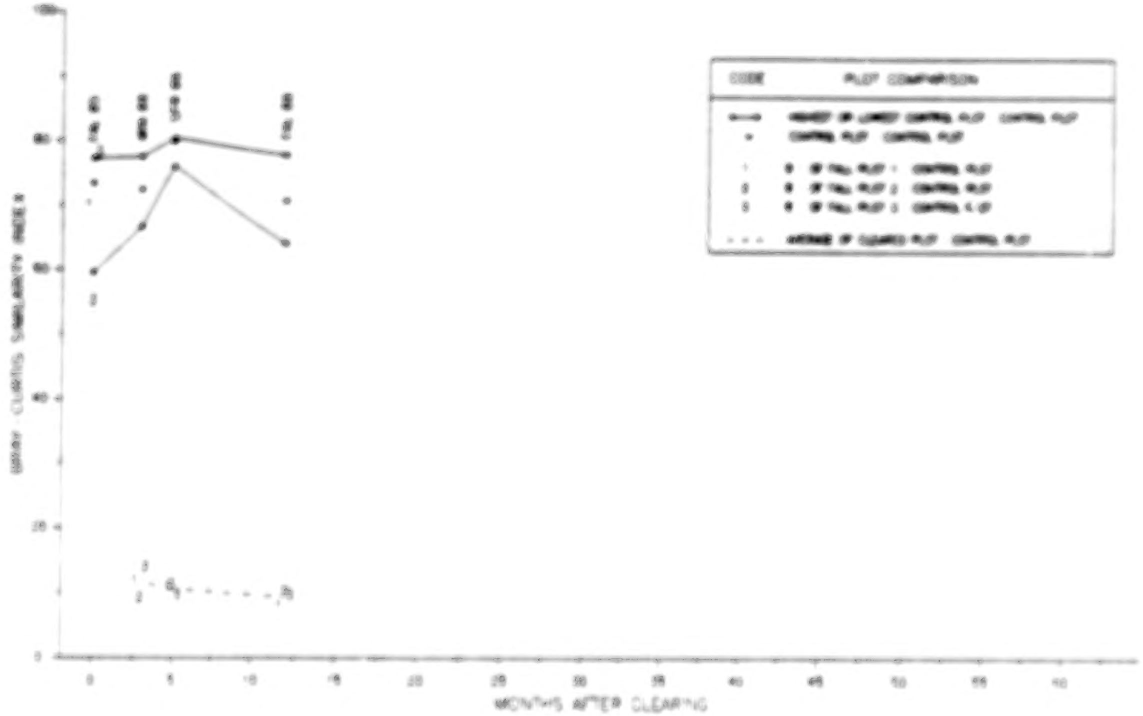


Figure I-61. *Mytilus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Pt. Sierra Nevada (E).

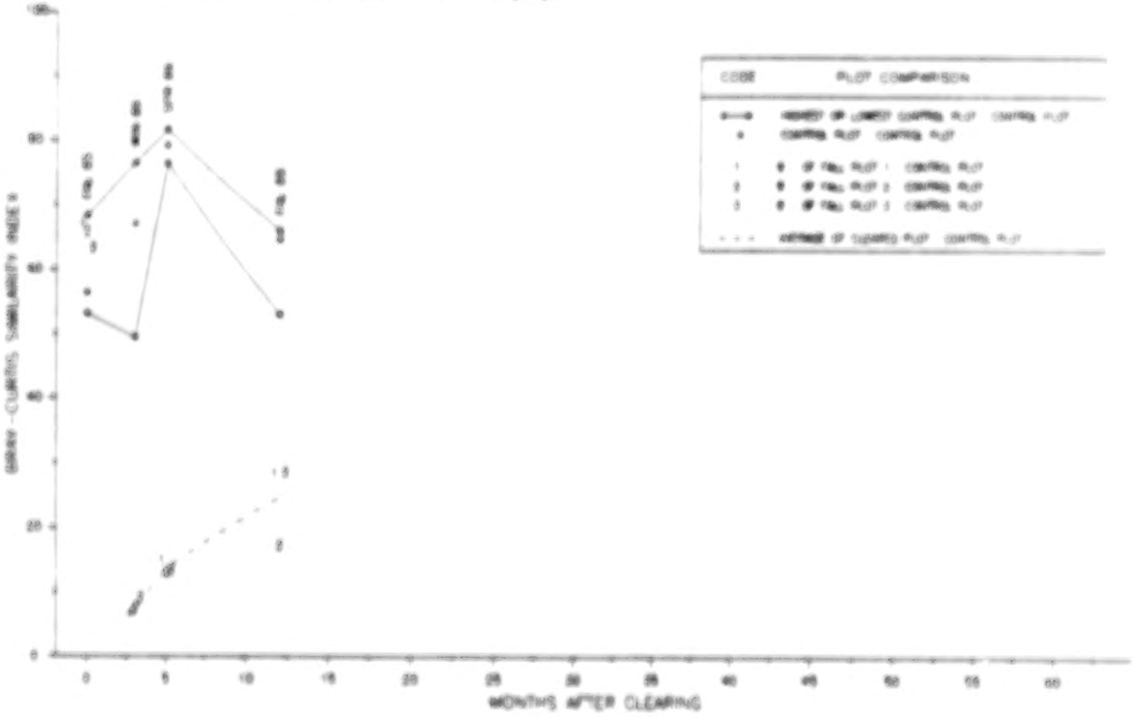


Figure I-62. *Mytilus* Assemblage: Bray Curtis Similarity between Fall-Cleared and Control Plots - Diablo Canyon (F).

Effects of Size and Severity of Disturbance: Results of Supplemental Study

A supplemental study on the effects of size and severity of disturbance on recovery is being performed in conjunction with the main study (see Appendix A). Focusing on one site (Pescadero Rocks, D) and assemblage (*Mytilus*), the supplemental study's objective is to investigate how recovery processes differ in clearings of different sizes and types. Experimental treatments include four different patch sizes (10 x 10 cm, 50 x 50 cm, 100 x 100 cm, and 150 x 150 cm) and two levels of clearing (completely cleared and partially cleared) at one time of year (fall). The results of the supplemental study as they relate to the findings of the main study are discussed here; the supplemental study is presented in full in Appendix A.

Results of the supplemental study show the size of clearing did not affect succession when edge effects were accounted for by subsampling the plot centers and borders (within 10 cm of the edge). Increased grazing by chitons in borders affected the distribution of some but not all species, depending on their specific tolerances to grazing and secondary interspecific competitive interactions. These results suggest that recruitment into the centers of patches may be independent of patch size within the range considered, and that the 25-cm wide buffer zone used in the main study is effective in avoiding edge effects.

The severity of disturbance did affect successional patterns in the supplemental study. In partially disturbed plots, more typical early successional species were less abundant than in completely disturbed plots and mid-successional species did not occur. Partially disturbed plots also showed no edge effects, and recovery tended to be more rapid than in completely cleared plots. These results suggest that results from early successional processes in the main study, where plots were completely cleared, may not be applicable to other situations with only partial clearings. Comparisons of results for later successional processes and final recovery will be made as succession continues.

Recovery patterns in the experimental plots in the *Mytilus* assemblage at Pescadero Rocks were similar for both the supplemental and main studies. Despite the one-year difference in clearing dates (fall 1984 for the supplemental study versus fall 1985 for the main study), similar successional trends were seen for the common taxa. At least at this site, recovery patterns did not vary from one year to the next for fall-cleared plots.

In the control plots, both the supplemental and main studies showed an increase in percent cover of mussels. Increased mussel abundance did not occur at any of the other sites in the main study. In a highly variable system, these results at Pescadero Rocks facilitate the comparison of these two studies. (Statistical comparisons of similarity were not done.)

Overall, results of the supplemental study indicate it may be possible to generalize among cleared patches of different sizes when edge effects are removed but, at least initially, it is probably not possible to generalize among clearings that differ in severity of disturbance. Recovery patterns do not necessarily differ among areas cleared in the same season during different years.

Conclusions

1. The control plots in the *Endocladia/Mastocarpus papillatus* assemblage have undergone few significant temporal changes during the two years of study, and changes that have occurred do not show any latitudinal trends. Seasonal and yearly changes in the species composition and abundance of the *Mytilus* assemblage were generally less than those in the *Endocladia/Mastocarpus papillatus* assemblage, and showed a similar lack of trends with latitude.

2. The spring-cleared plots in the *Endocladia/Mastocarpus papillatus* assemblage have completely recovered at Kibesillah Hill (A) after 12 months, and partially recovered (two of three plots) at Point Sierra Nevada and (one of three plots) at Diablo Canyon (F). The similarities of cleared plots to control plots have continually increased at most sites (Figures I-63 and I-64). Recovery rate appears generally unaffected by season of clearing, and does not indicate any overall trend with latitude (Figures I-63 and I-64). It may be inversely related to the abundance of ephemeral species that colonize during succession and to the species richness of a site.

3. After 12 months, only the fall clearings in the *Endocladia/Mastocarpus papillatus* assemblage at Point Sierra Nevada (E) had recovered, and this was associated more with changes in the control plots rather than changes in the cleared plots. Like the spring clearings, most of the fall clearings have continually increased in similarity to the controls (Figure I-64), but there is no indication that recovery rate is associated with latitude (Figure I-64). The similarity in the shapes of the spring-cleared and fall-cleared recovery curves (Figures I-63 and I-64) suggests that site-specific processes have a greater effect on succession in this assemblage than do season or latitude.

4. None of the spring clearings in the *Mytilus* assemblage have completely recovered, and similarities of clearings to controls at all sites is low (about 20 percent). Recovery has been much slower than the recovery of the spring clearings in the *Endocladia/Mastocarpus papillatus* assemblage. This difference is primarily attributable to the lack of mussel recruitment.

5. The similarity of fall-cleared plots to controls in the *Mytilus* assemblage is also very low after 12 months at all sites. The reasons for this lack of recovery appear similar to those suggested for the spring clearings in the *Mytilus* assemblage (4. above). The similarities of fall clearings to the controls were low and similar to each other at three and six months after clearing. They have increased between six and twelve months. Spring-cleared control similarities remained fairly constant after an initial increase at six months. This may be a reflection of slow initial colonization of species in the fall plots. Despite these seasonal differences, both spring and fall recovery curves have similar shapes (Figures I-65 and I-66), suggesting again that site-specific processes have a greater effect on recovery than does time of disturbance. Fall recovery rates also tend to decline with latitude (Figure I-66), but this trend may be confounded with differences in mussel abundance.

6. The results of the supplemental study in the *Mytilus* assemblage at Pescadero Rocks (D) indicate that the size of a clearing does not affect succession if the effects of edges (primarily caused by increased grazing in this study) are removed by not sampling within 10 cm of the edge of a plot (e.g., within a 10-cm-wide border). The width of this border may change with the kinds of grazers present, but these data suggest that edge effects in the main study are being minimized by not sampling within a 25-cm border

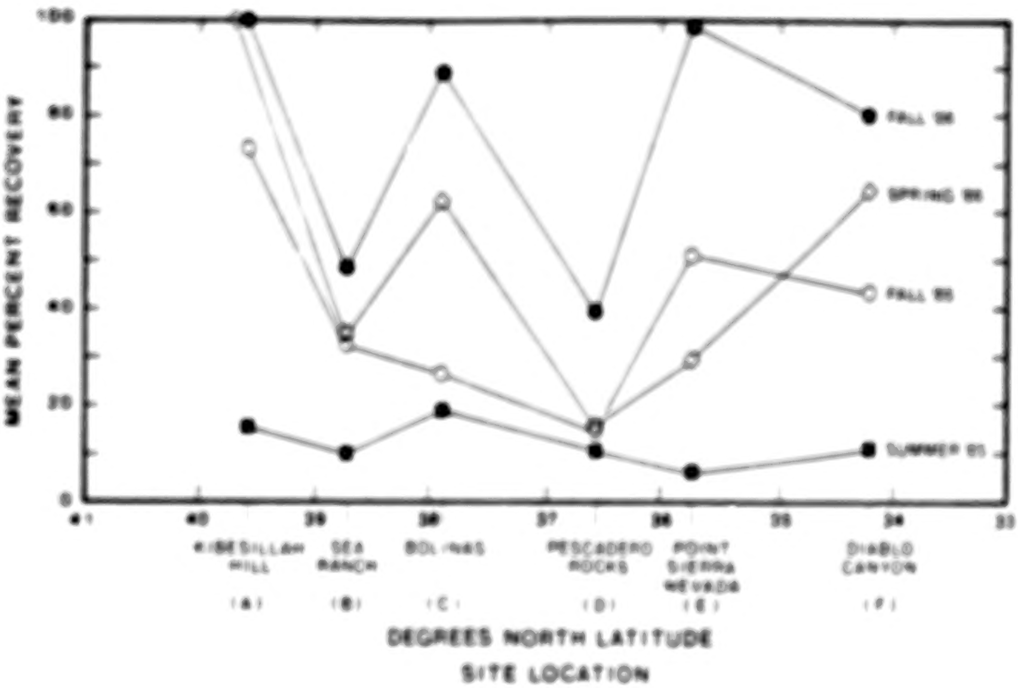


Figure 1-63. *Endocladia/Mastocarpus papillatus* Assemblage: Spatial and Temporal Variation in Percent Recovery of Spring-Cleared Plots (Mean of 3 Plots).

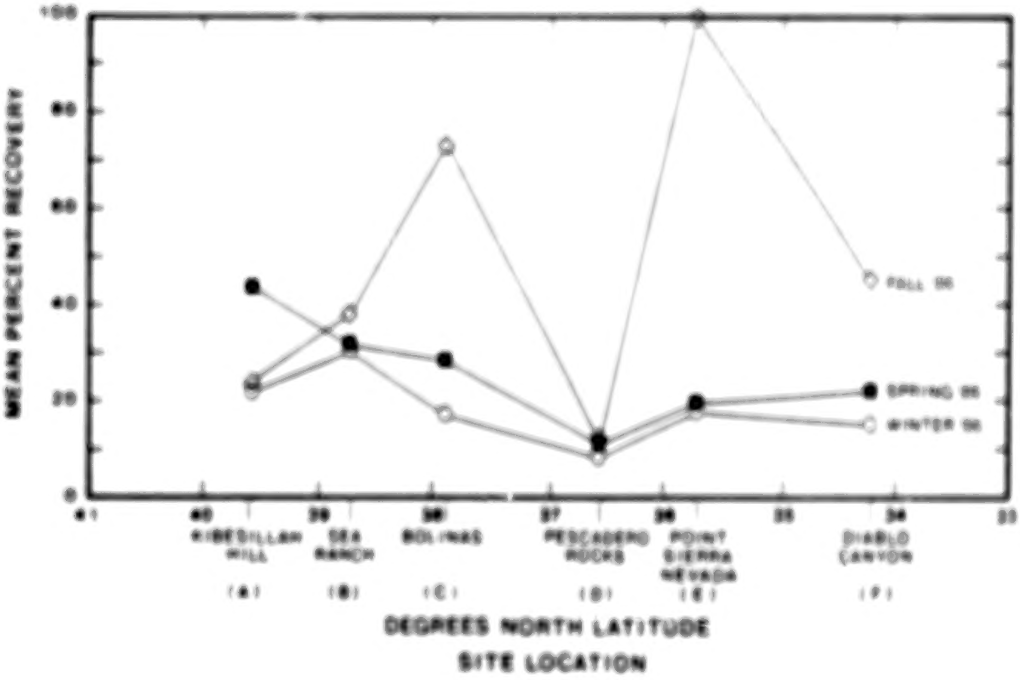


Figure 1-64. *Endocladia/Mastocarpus papillatus* Assemblage: Spatial and Temporal Variation in Percent Recovery of Fall-Cleared Plots (Mean of 3 Plots).

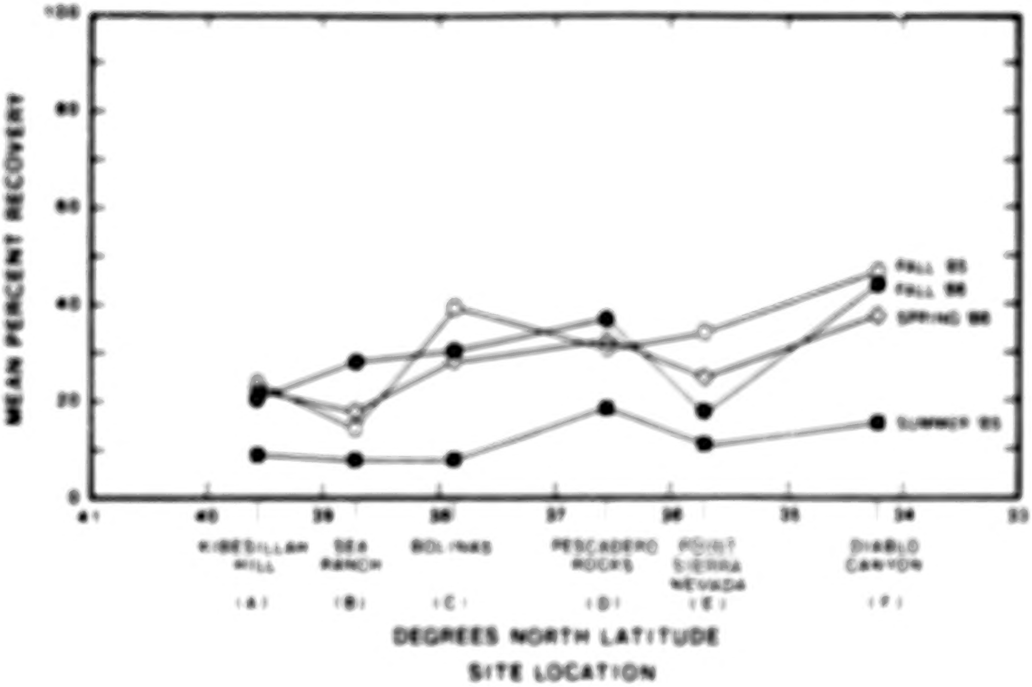


__Figure I-65__. *Mytilus* Assemblage: Spatial and Temporal Variation in Percent Recovery of Spring-Cleared and Plots (Mean of 3 Plots).

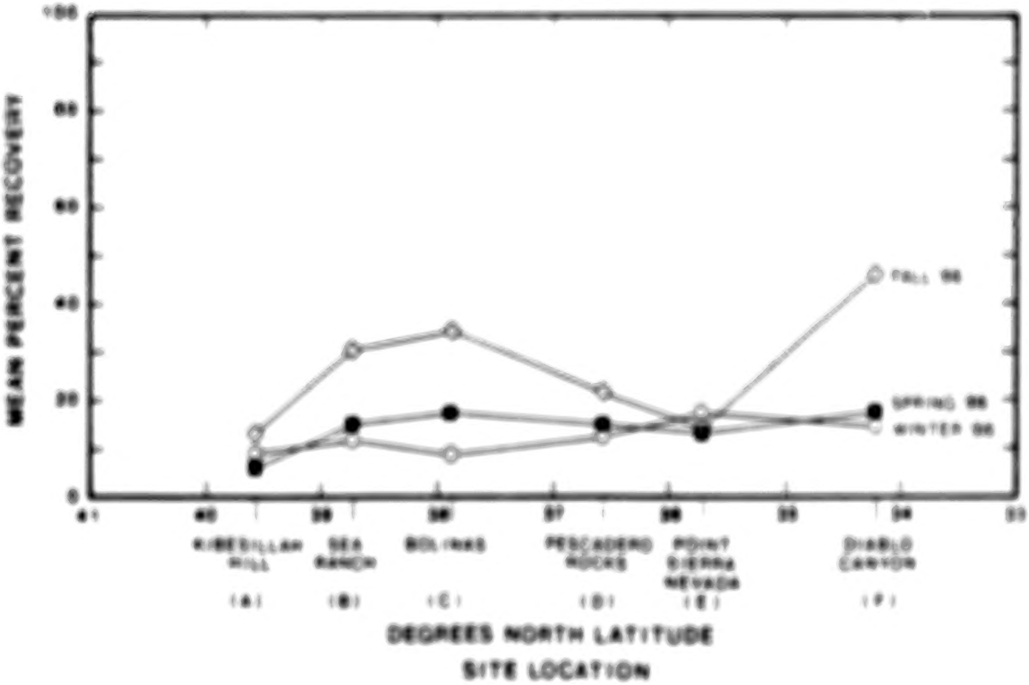


__Figure I-66__. *Mytilus* Assemblage: Spatial and Temporal Variation in Percent Recovery of Fall-Cleared Plots (Mean of 3 Plots).

around the plots. The supplemental study also showed that there are highly significant differences in species composition and recovery rate between completely and partially cleared plots during early successional processes. It may not be possible to generalize the results from complete clearings to clearings where disturbance is less severe.

PROJECT RECOMMENDATIONS

Objectives

The objective of the project recommendations is to address issues that arise during the course of the project which require further study or project changes, as well as to consider or develop mitigating measures for reducing the potential impact of offshore hydrocarbon development.

Status

Recommendations that were submitted with the Year I report (KLI, 1986) have been reviewed by the MMS. The primary focus of our recommendations was to increase measurements of important uncontrolled variables. In total, we had five recommendations for the project: (1) assessment of topographic relief at each site, (2) characterization of upwelling processes at each site, (3) continuation of the supplemental study on effects of size and severity of disturbance on recovery, (4) work-up of material from the cleared mussel plots, and (5) additional qualitative sampling.

All the recommendations except number 4, work-up of material from the cleared mussel plots, were approved by the MMS for implementation. A decision regarding recommendation 4 has not yet been made; we still feel that it would yield information valuable to the study. Recommendations 1 and 3 are currently in progress, recommendation 2 will be completed for the final report pending additional discussions with MMS staff, and recommendation 5 was completed in summer 1986.

At the present time, we have no additional recommendations for further study or changes to the project.

REFERENCES

Abbott, I.A. and G.J. Hollenberg. 1976. Marine algae of California. Stanford University Press, Stanford, CA. 827 pp.

Conceptual Software, Inc. 1985. PRODAS professional database analysis system; Database, statistics, graphics. Houston, Texas.

De Vogelaere, A.P. 1985. Effects of size, intensity, and edges of clearings on early rocky intertidal succession. Western Society of Naturalists. p. 27.

De Vogelaere, A.P. and M.S. Foster. 1986. Studies of the effects of size and severity of disturbance on the recovery of a rocky intertidal assemblage. Appendix F *in* Kinnetic Laboratories, Inc. Study of the rocky intertidal communities of central and northern California, Year I, prepared in association with the University of California, Santa Cruz, Moss Landing Marine Laboratories, and TERA Corporation for the Pacific OCS Region, Minerals Management Service, U.S. Dept. of the Interior. Contract No. 14-12-0001-30057. OCS Study, MMS 86-0051. 448 pp.

De Vogelaere, A.P. 1987. Rocky intertidal patch succession after disturbance: Effects of severity, size, and position. M.S. thesis, Moss Landing Marine Laboratories. 91 pp.

De Vogelaere, A.P. and M.S. Foster. 1988. Effects of size and severity of disturbance on the recovery of a rocky intertidal assemblage. Appendix A *in* Kinnetic Laboratories, Inc. Study of the rocky intertidal communities of central and northern California, Year II, prepared in association with the University of California, Santa Cruz, Moss Landing Marine Laboratories, and TENERA Corporation for the Pacific OCS Region, Minerals Management Service, U.S. Dept. of the Interior. Contract No. 14-12-0001-30057. OCS Study, MMS 89-0010. Vol. I of III.

Foster, M.S., A.P. De Vogelaere, C. Harrold, J.S. Pearse, and A.B. Thum. 1986. Causes of spatial and temporal patterns in rocky intertidal communities of central and northern California. Prepared for the Minerals Management Service, U.S. Dept. of the Interior by Kinnetic Laboratories, Inc. in association with the University of California, Santa Cruz, and Moss Landing Marine Laboratories under contract no. 14-12-0001-30057. Vols. 1 and 2. OCS Study, MMS 85-0049. 126 pp.

Foster, M.S., A.P. De Vogelaere, C. Harrold, K. Langan, J.S. Pearse, A.B. Thum, and D.A. Wilson. 1987. Annotated bibliography of successional and seasonal variation of the central and northern California rocky intertidal communities as related to natural and man-induced disturbances. Prepared for the Minerals Management Service, U.S. Dept. of the Interior by Kinnetic Laboratories, Inc. in association with the University of California, Santa Cruz, and Moss Landing Marine Laboratories under contract no. 14-12-0001-30057. OCS Study, MMS 86-0052. 651 pp.

Foster, M.S., A.P. De Vogelaere, C. Harrold, J.S. Pearse, and A.B. Thum. 1988. Causes of spatial and temporal patterns in rocky intertidal communities of central and northern California. Memoirs of the California Academy of Sciences 9:1-45.

Foster, M.S. 1989. The organization of algal assemblages in the northeast Pacific: The assumption of homogeneity and the illusion of generality. Hydrobiologia. In press.

Guiry, M.D., J.A. West, D.H. Kim, and M. Masuda. 1984. Reinstatement of the genus *Mastocarpus* Kutzing (Rhodophyta). Taxon 33(1):53-63.

Harrold, C. and D. Hardin. 1986. Prey consumption on land by the California sea otter, *Enhydra lutris*. Marine Mammal Science 2(4):309-313.

Kinnetic Laboratories, Inc. 1986. Study of the rocky intertidal communities of central and northern California, Year I. Prepared in association with the University of California, Santa Cruz, Moss Landing Marine Laboratories, and TERA Corporation for the Pacific OCS Region, Minerals Management Service, U.S. Dept. of the Interior. Contract No. 14-12-0001-30057. OCS Study, MMS 86-0051. 448 pp.

Lindberg, D.R. 1986. Name changes in the "Acmaeidae." The Veliger 29(2):142-148.

Masuda, M. 1982. A systematic study of the tribe Rhodomeleae (Rhodomelaceae, Rhodophyta). Journal of the Faculty of Science, Hokkaido University, Series V, 12(4):209-400.

Nigg, E.W. 1988. Reproductive periodicity and its relationship to recruitment and persistence of *Endocladia muricata* and *Mastocarpus papillatus*. M.S. thesis, Moss Landing Marine Laboratories. 36 pp.

Science Applications, Inc. 1979. Intertidal study of the southern California bight. Vol. I. Summary and synthesis of principal findings of the third-year southern California intertidal baseline study program. Prepared for BLM, U.S. Dept. of Interior, Washington, D.C.

Smith, R.I. and J.T. Carlton (Eds.). 1975. Light's Manual: Intertidal invertebrates of the central California coast. Third edition. University of California Press, Berkeley. 416 pp.

APPENDIX A

Effects of Size and Severity of Disturbance on the Recovery of a Rocky Intertidal Assemblage

Effects of Size and Severity of Disturbance on the Recovery of a Rocky Intertidal Assemblage

by

Andrew P. De Vogelaere[1]
and
Michael S. Foster

Moss Landing Marine Laboratories
P.O. Box 450
Moss Landing, CA 95039

---

[1] Present address: Institute of Marine Sciences
University of California
Santa Cruz, CA 95064

APPENDIX A

Effects of Size and Severity of Disturbance on the Recovery of a Rocky Intertidal Assemblage

TABLE OF CONTENTS

Page

LIST OF FIGURES I-97

LIST OF TABLES I-99

ABSTRACT I-101

TECHNICAL SUMMARY I-103

INTRODUCTION I-111

  Study Site I-112

METHODS I-115

  Experimental Design and Analyses I-115

  Clearing Techniques I-115

  Sampling Methods I-118

  Grazer Exclusion Experiment I-118

RESULTS I-119

  General Succession Patterns I-119

  Species Cover in Complete Disturbances - Effects of Size and Position I-124

  Differences Between Replicate Plots and Spore Dispersal Distances I-135

  Effects of Position in Partial Disturbances I-135

  Complete Versus Partial Disturbances I-135

  Grazer Abundance I-144

  Chiton Exclusion Experiment I-144

  Incidental Evidence Confirming the Results of the Grazer Experiment I-147

APPENDIX A

TABLE OF CONTENTS (Continued)

Page

DISCUSSION I-151

Partial Versus Complete Disturbances I-151

Effects of Patch Size and Position Within Patch I-151

General Perspectives I-153

REFERENCES I-155

APPENDICES I-161

LIST OF FIGURES

Figure		Page
I-A-A.	Study site showing OCS planning area and region.	I-109
I-A-1.	Location of study site: Pescadero Rocks, Carmel Bay, California.	I-113
I-A-2 a,b.	General successional patterns found in the centers of a) completely disturbed and b) partially disturbed 50 x 50 cm plots.	I-120
I-A-3.	Mean percent cover (±1 SD, n=12) through time of common organisms in control plots.	I-122
I-A-4 a-g.	Percent cover [±1 SD of replicate plots (n=4), calculated by combining sub-samples] through time of a) total cover, b) *Ulva* sp(p)., c) *Porphyra perforata*, d) *Egregia menziesii*, e) *Iridaea flaccida*, f) *Bossiella plumosa* and g) pink crusts in different sized plots, and in different positions within completely cleared plots.	I-125
I-A-5 a-e.	Percent cover [±1 SD of replicate plots (n=4), calculated by combining subsamples] through time of a) total cover, b) *Ulva* sp(p)., c) *Porphyra perforata*, d) *Bossiella plumosa*, and e) pink crusts in completely versus partially disturbed 50 x 50 cm plots, and differences between positions within each plot type.	I-136
I-A-6 a,b.	Mean densities (±1 SE, area=100 cm^2, n=4 for 10 x 10 cm or n=18 for others) of a) the chiton, *Nuttallina californica*, and b) limpets in different positions within completely disturbed plots through time.	I-145
I-A-7.	Mean (±1 SE, area=100 cm^2, n=18) chiton (*Nuttallina californica*) densities in different positions within partially cleared plots through time.	I-146
I-A-8.	Algal succession in the presence and absence of chiton grazing.	I-146
I-A-9 a-b.	Percent cover [±1 SD; n=4 for 10 x 10 cm plots, n=12 for lumped borders and centers of other plot sizes] through time of a) barnacles (*Balanus* and *Chthamalus* combined) and b) *Cylindrocarpus rugosus*.	I-149

LIST OF TABLES

Table		Page
I-A-1.	Patch sizes found in mussel communities of the northeastern Pacific.	I-116
I-A-2.	Design of patch size and severity experiment.	I-117
I-A-3.	List of species that colonized completely cleared and partially cleared plots.	I-121
I-A-4.	Sessile organisms found in control plots.	I-123
I-A-5.	Results of analyses of variance on the effects of plot size, position within plot (border vs. center) and replicate plots on species abundance through time.	I-132
I-A-6.	Results of analyses of variance on the effects of disturbance severity, position within plot (border vs. center) and replicate plots on species abundance through time.	I-141
I-A-7.	Effect of *Nuttallina californica* grazing on barnacle abundances (x ± 1 SD, 100 cm^2 areas) through time.	I-148

ABSTRACT

Disturbances produce a mosaic of patches in mussel assemblages throughout the northeastern Pacific. Two parameters that affect structure within these patches are size and severity of disturbance. Completely disturbed patches rely on surrounding areas for sources of recruits, while partially disturbed patches have survivors and propagules that may still be able to grow. In this study, the effects on succession of different levels of disturbance severity and patch size were examined with experimental clearings. The clearings were subsampled in borders and centers to distinguish between size and edge effects. This report covers the first two years (1984-1985) of a five-year study (1984-1989).

Successional patterns depended on the severity of disturbance. In partially disturbed plots, early successional species were reduced in abundance, mid-successional species did not occur, edge effects were lacking, and recovery tended to be more rapid than in completely disturbed plots. The basal crust-upright frond algal morphology, often suggested as resistant to grazing, was found to be well suited to habitats with less severe disturbances. Fronds rapidly regenerated from crusts in the partially disturbed clearings.

Patch size (10 x 10 cm to 150 x 150 cm) did not affect species abundances except at the size small enough to have no functional center. Edge effects, attributed to increased chiton (*Nuttallina californica*) densities, varied among algal species. Increased grazing enhanced some resistant species abundances probably by reducing competition with species less tolerant to grazing. Some algae demonstrated no edge effect.

STUDY TITLE: Successional and Seasonal Variation of Central and Northern California Rocky Intertidal Communities as Related to Natural and Human-Induced Disturbances.

REPORT TITLE: Effects of Size and Severity of Disturbance on the Recovery of a Rocky Intertidal Assemblage.

CONTRACT NUMBER(S): MMS 14-12-0001-30057 (Supplemental study).

SPONSORING OCS REGION: Pacific.

APPLICABLE PLANNING AREA(S): Central and northern California.

FISCAL YEAR(S) OF PROJECT FUNDING: 1984, 1986 (Supplemental study).

COMPLETION DATE OF REPORT: December 1988.

COST(S): (Supplemental study) FY1984: $25,000; FY1986: $38,743.80; CUMULATIVE PROJECT COST: $63,743.80.

PROJECT MANAGER(S): (Supplemental study) D. Hardin.

AFFILIATION: Kinnetic Laboratories, Inc.

ADDRESS: Kinnetic Laboratories, Inc., P.O. Box 1040, Santa Cruz, CA 95061.

PRINCIPAL INVESTIGATOR(S):* (Supplemental study) A. De Vogelaere.

KEY WORDS: Central California; biology; rocky intertidal; mussels; *Mytilus*; succession; disturbance; algae; clearing; community structure.

BACKGROUND: In light of potential oil and gas operations off the central and northern California coast, the MMS is interested in obtaining information on the sensitivity of intertidal communities to disturbance by oil spills. A major study is being performed to investigate seasonal and successional variation in rocky intertidal communities and determine the response of these communities to natural and human-induced disturbances. The present study was designed to supplement the main study by providing information on biological effects of different clearing methodologies. With this information, it may be possible to extrapolate from the experimental manipulations of the main study to other disturbance scenarios.

OBJECTIVES: The objective of this study is to investigate how recovery processes differed in clearings of different sizes and types.

DESCRIPTION: The study was initiated in the mussel assemblage at Pescadero Rocks in the fall of 1984. This report desbribes progress on the first two years (1984-1985) of a five-year study ending in 1989. The study design includes clearing patches of four sizes (10 x 10, 50 x 50, 100 x 100, 150 x 150 cm) and using two clearing types (completely sterilized and partially cleared). Sampling

of percent cover of species is performed bimonthly in the borders and centers of each plot.

SIGNIFICANT CONCLUSIONS: Species abundances did not differ significantly in cleared areas within the size range of 50 x 50 to 150 x 150 cm when border effects are accounted for by subsampling. The 25-cm wide buffer zone used in the main study is effective in avoiding edge effects. However, at least in early succession, it is probably not possible to generalize among clearings that differ in severity (disturbance type). Recovery patterns do not necessarily differ between years when they are cleared at the same season.

STUDY RESULTS: The size of clearing did not affect succession when edge effects were accounted for by subsampling plot centers and borders (more than 10 cm from the edge). Increased chiton grazing in the borders affected the distribution of some but not all species, depending on their tolerances to grazing and secondary interspecific competitive interactions. The results indicate that recruitment into the centers of patches is independent of patch size within the range considered.

Severity of disturbance did affect successional patterns. In partially cleared plots, more typical early successional species were less abundant than in completely disturbed plots and mid-successional species did not occur. Partially cleared plots also showed no edge effects, and recovery tended to be more rapid than in completely cleared plots.

Recovery patterns in the Mytilus assemblage at Pescadero Rocks were similar for both the supplemental and main studies. Despite the one-year difference in clearing dates (fall 1984 versus fall 1985), similar successional trends were seen for the common taxa. In the control plots, both studies showed a similar increase in the percent cover of mussels.

STUDY PRODUCTS:

De Vogelaere, A.P. 1985. Effects of size, intensity, and edges of clearings on early rocky intertidal succession. Western Society of Naturalists: 66th Annual Meeting Program/Abstracts. Monterey Conference Center, Monterey, California. p. 27.

De Vogelaere, A.P. and M.S. Foster. 1986. Studies of the effects of size and severity of disturbance on the recovery of a rocky intertidal assemblage. Appendix F in Kinnetic Laboratories, Inc. Study of the rocky intertidal communities of central and northern California, Year I, prepared in association with the University of California, Santa Cruz, Moss Landing Marine Laboratories, and TERA Corporation for the Pacific OCS Region, Minerals Management Service, U.S. Dept. of the Interior. Contract No. 14-12-0001-30057. OCS Study, MMS 86-0051. 448 pp.

De Vogelaere, A.P. 1987. Rocky intertidal patch succession after disturbance: Effects of severity, size, and position. M.S. thesis, Moss Landing Marine Laboratories, California. 91 pp.

De Vogelaere, A.P. and M.S. Foster. 1988. Effects of size and severity of disturbance on the recovery of a rocky intertidal assemblage. Appendix A in Kinnetic Laboratories, Inc. Study of the rocky intertidal communities of central and northern California, Year II, prepared in association with the University of California, Santa Cruz, Moss Landing Marine Laboratories, and TENERA Corporation for the Pacific OCS Region, Minerals Management Service, U.S. Dept. of the Interior. Contract No. 14-12-0001-30057. OCS Study, MMS 89-0010. Vol. I of III.

* P.I.'s affiliation may be different than that listed for Project Manager(s).

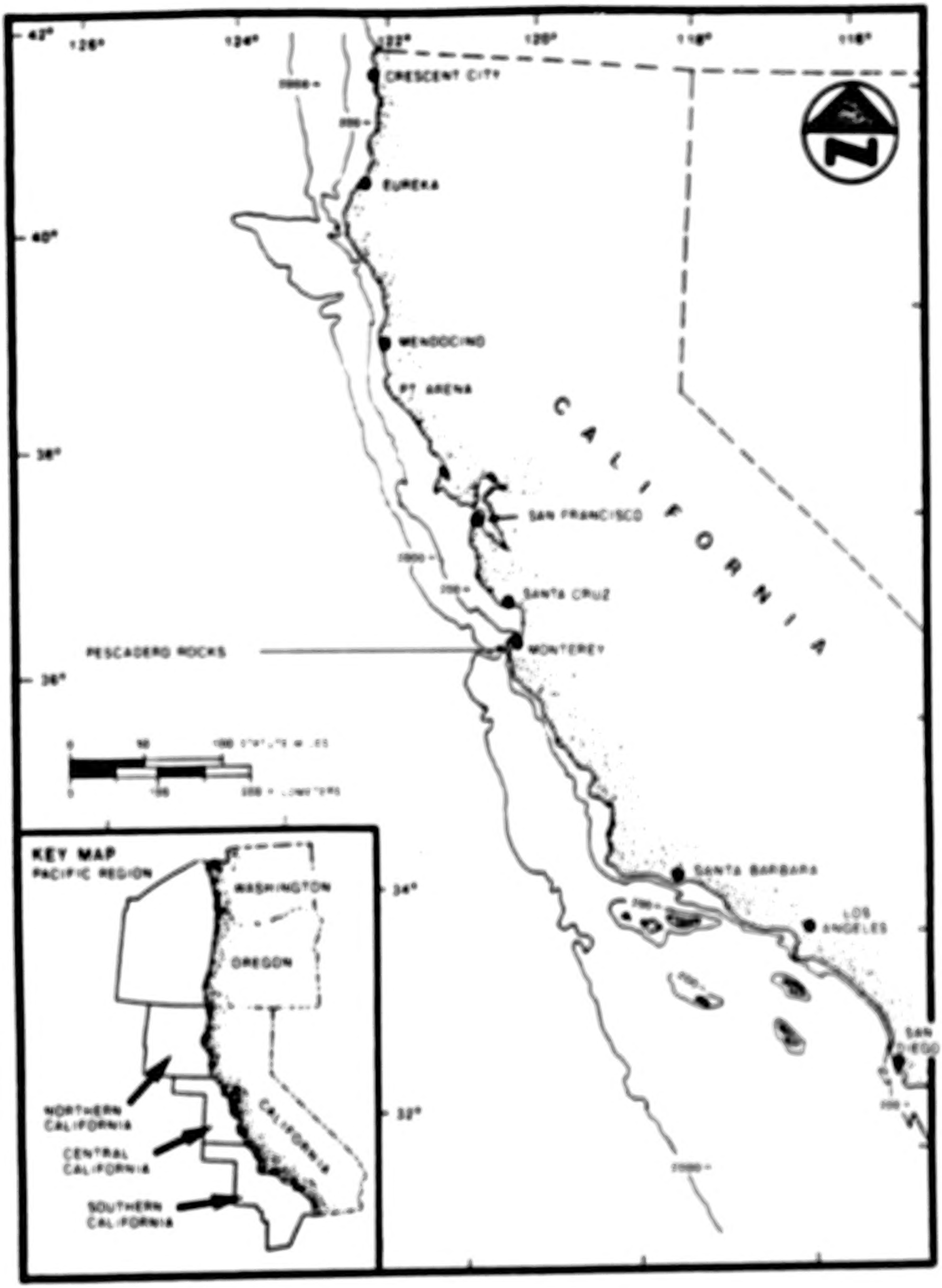


Figure I-A-A. Study site showing OCS planning areas and region.

INTRODUCTION

The structure and organization (sensu Menge, 1976) of many communities are influenced by disturbances (see reviews by Wiens, 1976; Whittaker and Levin, 1977; Connell, 1978; White, 1979; Sousa, 1984a; Pickett and White, 1985). These disturbances, whether physical or biological, affect relative abundances of species and can regulate spatial and temporal heterogeneity. If the disturbance regime meets certain criteria of regularity, it may be an important factor in natural selection (Harper, 1977; Denslow, 1980; Runkle, 1985; Christensen, 1985; but see Sousa, 1984a). Important disturbance parameters are frequency, seasonality, severity and size. If disturbances are viewed as creating patches within the community, the area and frequency of patch formation give an idea of the pervasiveness of disturbances at the community level. At the within-patch level, season of patch creation has been demonstrated to be important to the structure of some, but not all communities (Sousa, 1984a). The focus of this study is on the effects of severity and size of disturbance on succession within patches.

Disturbance severity (sensu Sousa, 1984a) is a measure of damage done. Two levels of severity were examined in the present study: complete and partial disturbance. Partially disturbed areas retain the ability of regrowth from remaining organisms or propagules (e.g., understory seedlings after a windthrow, Bormann and Likens, 1979; recovery of some salt marsh plants after wrack deposition, Bertness and Ellison 1987; fauna left in grey whale feeding pits, Oliver and Slattery, 1985). Complete disturbances result in sterile surfaces dependent on surrounding undisturbed areas as sources of recruits (e.g., ice scour, O'Clair, 1981; forest land slides, Garwood *et al.*, 1979; lava flow, Doty, 1967).

Different levels of severity are most often discussed in fire-regulated communities (Sousa, 1984a; Christensen, 1985) and recently some subtidal coral communities (Connell and Keough, 1985). As shrubland communities get older, the ratios of their dead to live material increase, causing more intense and severe fires (Green, 1982; Christensen, 1985). These fires often result in partial disturbances, because the plants are adapted to regrow from remaining subterranean buds. In addition, the fire may stimulate seed germination (Christensen, 1985). Zedler *et al.* (1983) found that repeated fires reduced plant regrowth capabilities and caused long-term community changes that could explain much of the pattern in southern California shrub vegetation. In coral communities, storms fragment organisms into pieces that can regenerate unless the severity is such that all living tissue is abraded (Connell and Keough, 1985). Connell and Slatyer (1977) have proposed that long-term successional events depending on new recruitment will occur after severe, large disturbances, while vegetative growth processes dominate after small, less severe disturbances.

The rocky intertidal ecosystem is well-suited for manipulative studies on the effects of different disturbance severities. Complete disturbances occur from rock shear and when conglomerate rocks fall out of sandstone matrices. Though complete disturbances have been suggested to be rare (Sousa, 1985), they have been observed by the authors throughout the central and northern California coast. The literature may suggest they are rare because many studies have been conducted on granite and volcanic rock where shear and dislodgement are less likely to occur. Another form of complete clearing is found in thick-layered mussel beds and results from logs (Dayton, 1971), waves (Paine and Levin, 1981; Sousa, 1984b) and sea otters (VanBlaricom, 1987) removing clumps of mussels. Though the possibility of propagules remaining after the disturbance has not been ruled out, it seems unlikely in cases where anoxic sediments are found at the base of mussel beds. Partial clearings are found after wave shear leaves remnants of basal crusts and propagules (Dayton, 1975; Lubchenco and Menge, 1978; Lubchenco, 1980; Dethier, 1984; Foster and Sousa, 1985; Foster *et al.*, 1988). Other agents of partial disturbances are desiccation (Sousa, 1979; Foster *et al.*, 1988) and seal haul out (Boal, 1980; De Vogelaere, personal observation). Though partial disturbances are less well documented, they are probably found in all places where algae occupy substratum in assemblages in which thick mussel matrices are not formed.

The effects of disturbance size on succession have recently been investigated in a mussel-dominated rocky intertidal zone (Sousa, 1984b) and in a subtidal community of clonal organisms (Keough, 1984). Sousa (1984b) found that increased grazing intensity influenced algal succession in relatively small clearings in a mussel bed. Grazer-resistant but competitively inferior species were found in small patches, while grazer-vulnerable but competitively superior species were found in large patches. Keough (1984) found that size was not important if surrounding organisms were able to quickly occupy open areas by vegetative growth. In the absence of vegetative growth (e.g., isolated patches, sensu Sousa, 1985), species composition in small patches depended on recruitment patterns of planktonic larvae, while larger patch composition was determined by competition after recruitment. Qualitative observations indicate that large patches may exhibit edge effects related to differences in grazing, recruitment, and vegetative ingrowth (Suchanek, 1978; Paine and Levin, 1981; Sousa, 1984b). Our understanding of size effects on succession within patches could be enhanced by subdividing large areas into edges and centers.

The primary objective of this study was to determine the effects of variable disturbance regimes on successional processes within an intertidal mussel assemblage by creating complete and partial disturbances of various sizes and subsampling edges and centers. An additional objective was to examine certain assumptions of other manipulative intertidal field experiments. In many of these studies, the size and method of clearing was chosen as a matter of convenience, tacitly assuming variations in these factors would be irrelevant to the question being investigated (e.g., Northcraft, 1948; Cross and Southgate, 1983). By comparing different disturbance regimes, the validity of these assumptions were tested at one site. This report covers the first two years (1984-1985) of a five-year supplemental study ending in October 1989. It includes the results of the study's first year which were reported previously (Appendix F in Kinnetic Laboratories, Inc. 1986).

Study Site

The study site is located on Pescadero Rocks in Stillwater Cove, Carmel Bay, central California (36°34'N, 121°56'W; Figure I-A-1). Because it is an island, public access is very limited. Stillwater Cove opens to the south, providing some protection from large northwesterly winter swells. According to the descriptions of Ricketts *et al.* (1985) the exposure may be characterized as protected outer coast, but during the months of December and January it was often impossible to sample due to large waves.

The experimental site is a flat 519 m^2 bench with a tidal height range of approximately 1.0 to 1.3 m (3.28 to 4.26 ft) above mean lower low water. The substratum is composed of conglomerate rocks protruding from a sandstone matrix. The conglomerates are composed primarily of silicic volcanic rocks while the sandstone is composed from an igneous-granite source cemented by calcite, making the rocks only moderately porous (P. Ramirez, personal communication).

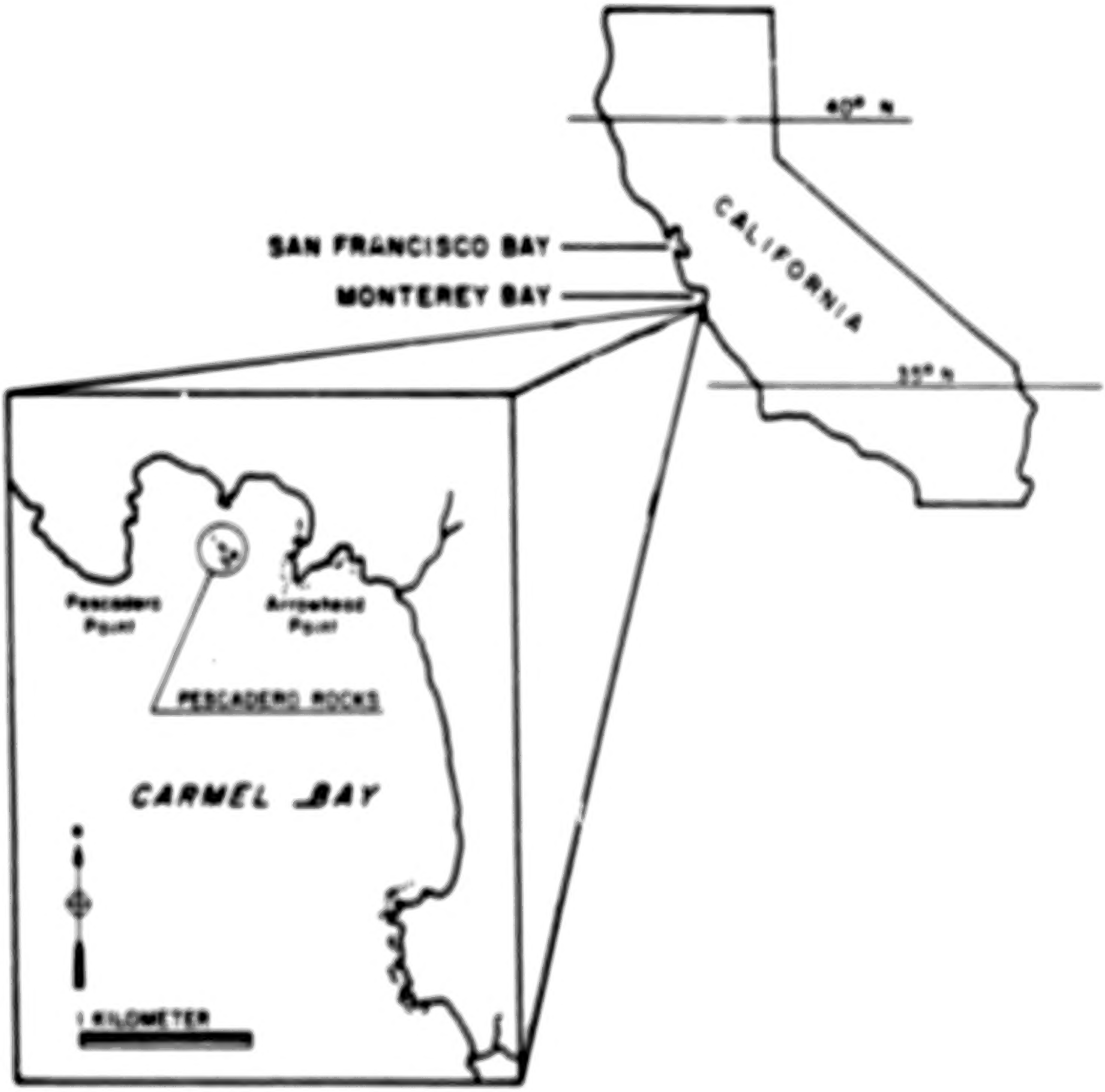


Figure I-A-1. Location of study site: Pescadero Rocks, Carmel Bay, California (36°34'N, 121°56'W).

The assemblage cover (see Results for details) consisted of 45 percent *Mytilus californianus*, 15 percent *Bossiella plumosa*, 15 percent *Tetraclita rubescens* and various less abundant algae. In contrast to algae in some mussel assemblages, most of these algae were not epizoic. Large sea stars (*Pisaster ochraceus*) were rare, ranging from 0 to 4 individuals on the experimental site per visit. Observed physical disturbances that created patches consisted of wave shear removing mussels, conglomerate rocks falling out of the sandstone, and periodic rock shear. Representative patch sizes for each type of these natural disturbances during the study period were 18-400 cm^2, 9-70 cm^2, and 36-60 cm^2, respectively.

METHODS

Experimental Design and Analyses

Before initiating the experiment, criteria were developed for the size and shape of plots to be used, how they would be cleared, and what to consider as the border of a plot. Square plots were chosen because this is the most common shape used in intertidal work. The size range of 10 to 150 cm on a side was selected because it includes most common, natural patch sizes in northeastern Pacific mussel beds (Table I-A-1) and areas often used for experimental manipulations (De Vogelaere, in prep.). Partial clearing was chosen to mimic removal of organisms by waves, and complete clearing was chosen to mimic rock shear, common experimental manipulations (see Clearing Techniques below), and probably disturbance in thick mussel beds with anoxic sediments at their base (see Introduction). Finally, border width was chosen as 10 cm because a pilot clearing demonstrated this region differed from the center in having relatively low algal cover.

A multi-factor design and subsampling were used (Table I-A-2). The four sizes of complete clearings (10, 50, 100, 150 cm on a side) and one size of partial clearing (50 cm on a side) were randomly assigned to the site with a grid system, and adjusted so they would be at least one meter apart. Each plot was marked with stainless steel bolts and epoxy. The plots were subsampled (see Sampling Methods) to give some independence of samples through time and to facilitate comparisons between different size plots. There were four replicates of each plot type. Only one size of the partial clearing was used because of site size limitations and logistic constraints.

Analyses consisted of compiling species lists, trends in species cover, and multi-factor analyses of variance (Winer, 1971). An arcsine transformation was used to normalize data and an F max text was used to check for equality of variances (Sokal and Rohlf, 1981). For trends and analyses, only species which at one time had a mean cover (over all plots) of greater than 10 percent were considered. The 10 x 10 cm plots were analyzed only graphically because they are too small to subsample and, by definition, are all border and no center (see Table I-A-2).

Clearing Techniques

To make complete clearings, all large organisms were removed with a chisel, the plots were scrubbed with a wire brush, and the substratum was repeatedly burned with a propane torch. Between burns the plots were wire brushed and standing water was sponged away. A hand-size torch was used on the 10 x 10 and 50 x 50 cm plots and a large weed burner torch was used on the larger plots. To maintain a distinct edge without singeing the surrounding organisms, numerous wet rags were placed around the plots and covered with wet sheets of plywood. When all of the plots were cleared, a final burning was performed to ensure a uniform experimental starting time.

To create partial clearings, mussels and barnacles were chipped away with a chisel without striking the substratum, and upright algae were pulled by hand until only their holdfast or crustose portions remained; there was no brushing or burning.

Table I-A-1. Patch sizes found in mussel communities of the northeastern Pacific.

Location[1]	Patch Size (m^2) mean	Patch Size (m^2) range	Reference (latitude)
Washington:			Dayton, 1971[2]
Tatoosh Island,	4.5	0.5 - 16.0	(48°24'N)
Portage Head,	0.05	0.03 - 0.09	(48°17'N)
Shi Shi Reef	2.7	0.5 - 8.1	(48°16'N)
Washington:			Dayton, 1973
Tatoosh Island	6.0	0.3 - 26.3	(48°24'N)
Washington:			Paine, 1981[3]
Mukkaw Bay,	0.03	2×10^{-4} - 1.68	(48°19'N)
Shi Shi Beach,	0.03	" - 1.85	(48°16'N)
West Island,	0.33	" - 12.87	(48°24'N)
Strawberry	0.18	"• - 26.47	(48°24'N)
California:			Sousa, 1984b
Bodega Head	0.21	0.01 - 1.13	(38°18'N)
California:			VanBlaricom, 1987
Pt. Piedras Blancas	0.25	0.03 - 1.34	(35°40'N)

---

[1] Studies are listed according to date published but also reflect a gradient from north to south.

[2] Calculations made from "ultimate sizes" in Table 2 of Dayton (1971).

[3] Means calculated from winter samples in Table 1 and ranges obtained from text and Figure 3 in Paine and Levin (1981).

• Approximate size of one mussel.

Table I-A-2. Design of Patch Size and Severity Experiment.

Plot Size	Treatment	Size of Border	No. of Plots	No. of 100 cm^2 Quadrats Sampled Within Each Plot
150 x 150 cm	Complete Clearing	10 cm	4	3 - Center, 3 - Border
100 X 100 cm	Complete Clearing	10 cm	4	3 - Center, 3 - Border
50 X 50 cm	Complete Clearing	10 cm	4	3 - Center, 3 - Border
10 X 10 cm	Complete Clearing	Entire Plot	4	1 (Entire Plot)
50 X 50 cm	Partial Clearing	10 cm	4	3 - Center, 3 - Border

Sampling Methods

A point quadrat was used to measure the percent cover of organisms bimonthly over a two-year period. It consisted of a plexiglass grid of 100 evenly spaced holes in a 10 x 10 cm area and three large holes for adjustable legs. The legs held the plexiglass sheet 15 cm above and parallel to the substratum so the organisms below could be easily identified. A pin was lowered through ten randomly selected holes in the grid and the layers of organisms contacted below the grid were identified and recorded. At each sampling date, new coordinates were chosen to place three quadrats randomly within each border and center of the plots. In addition, a new set of random holes in the 10 x 10 cm grid was selected. Alternate points on the grid were used if the pin came in contact with a pool of standing water; this minimized habitat variability that seemed to influence grazing processes.

Grazers were counted on each sampling date in two plots of each size and type of clearing. They were sampled haphazardly by tossing three 10 x 10 cm quadrats in each border and center. This was accomplished for borders by adjusting quadrats in the centers of plots to the closest border position. The number and size ranges of limpets (< or > 5 mm) and chitons (< or > 10 mm) were noted. Other grazers were rare and only noted qualitatively. The entire area of all 10 x 10 cm clearings was sampled.

At each sampling period, the plots were photographed and qualitative observations were made. As necessary, voucher specimens were collected.

Grazer Exclusion Experiment

Initial observations indicated the chiton *Nuttallina california* was affecting the borders of plots (see Results). To test this effect experimentally, nine 10 x 10 cm plots were completely cleared as described earlier. Three replicates of each of three treatments were randomly assigned to the plots. The treatments were a fence excluding molluscan grazers, a fence including four *N. californica*, and no fence. The chiton density was determined from counts made in the borders of the previously cleared plots (see Results). Because it has been suggested that grazers seek refuge in surrounding mussels during low tide (Suchanek, 1978; Sousa, 1984b), this may be a conservative estimate. Fences were made of folded 2 mm plastic mesh attached with fiberglass rods, bolts, and Splash Zone™ epoxy. Differences in succession between the fence treatments with and without chitons could be ascribed to *N. californica* grazing. The non-fence treatment allowed for qualitative comparisons between fence treatments and the clearing type used in the main experiment [for a discussion on fence-cage effects, see Underwood (1980)]. The plots were sampled with point quadrats as described earlier. In addition, barnacles were counted.

RESULTS

General Succession Patterns

The successional pattern in completely disturbed plots was typical of that found in other intertidal studies. It was initiated with dominance by a few ephemeral species, and diversity increased with the advent of perennial species (Sousa, 1979; Sousa, 1984b; Paine and Levin, 1981; Figure I-A-2a, Table I-A-3). Benthic diatoms were the first visible organisms in the plots. Their abundance was not quantified because it fluctuated from 0 to 100 percent cover in a matter of days, depending on the weather. *Ulva* sp(p). (mostly *U. lobata*) and *Porphyra perforata* filled the plots within a few months (Figure I-A-2a), the latter often forming a layer over the former. Coincidental with the decline of *Ulva* and *Porphyra*, the perennial algae *Egregia menziesii*, *Bossiella plumosa*, and *Iridaea flaccida* became established. Pink crusts also established at this time and were probably the basal crust of *B. plumosa* and, perhaps, *Corallina* sp(p). All have a similar basal morphology. At the end of the study period, one of the intermediate perennials (*E. menziesii*) was declining and one of the later successional species (*B. plumosa*) was well established. As succession continues, diversity may decrease as mussels become established (Connell, 1978; Paine and Levin, 1981).

Mytilus californianus entered the plots as adults, presumably rolling into pockets and cracks, then re-attaching. Rates of horizontal movement of mussels from the edges of plots have been associated with the thickness of the surrounding mussel bed (Paine and Levin, 1981; Suchanek, 1985). The dispersed nature of the mussel matrix at this site may account for the negligible mussel encroachment observed as compared to other studies (Paine and Levin, 1981; Sousa, 1984b). Although numerous mussel recruits (individuals 1-2 mm in length, too small to identify to species) were observed at higher tidal levels in an *Endocladia muricata* assemblage, they were rare in the experimental plots. Both Suchanek (1978) and Sousa (1984b) found few *M. californianus*, but *M. edulis* were common in their patches. Additional species that colonized the patches in low abundances are listed in Table I-A-3.

The succession pattern in the partially disturbed plots was distinctly different from the pattern in completely disturbed plots initially, but eventually they were similar for the dominant late successional alga (Figure I-A-2b). At the outset, basal crusts and perhaps propagules remained after the partial disturbance and the initial diatom bloom was suppressed. *Ulva* species and *Porphyra perforata* became abundant but less so than in the complete disturbances, and at a comparatively later date for *Ulva*. The intermediate perennial macroalgae did not appear. As in the complete disturbances, *Bossiella*, the late successional species, became prominent as it developed from the basal crusts. The resurgence of *Ulva* species in both types of disturbances may have been more related to seasonal than successional changes. *Ulva* grows well as an epiphyte on *Bossiella* at this site during foggy summer months when waves are apparently less effective at dislodging it.

In the control plots, total cover stayed at about 90 percent while relative abundances of the three dominant species changed (Figure I-A-3, Table I-A-4). *Mytilus californianus*, a known competitive dominant in Washington (Paine, 1974), seemed to be replacing *Bossiella plumosa* and *Tetraclita rubescens*.

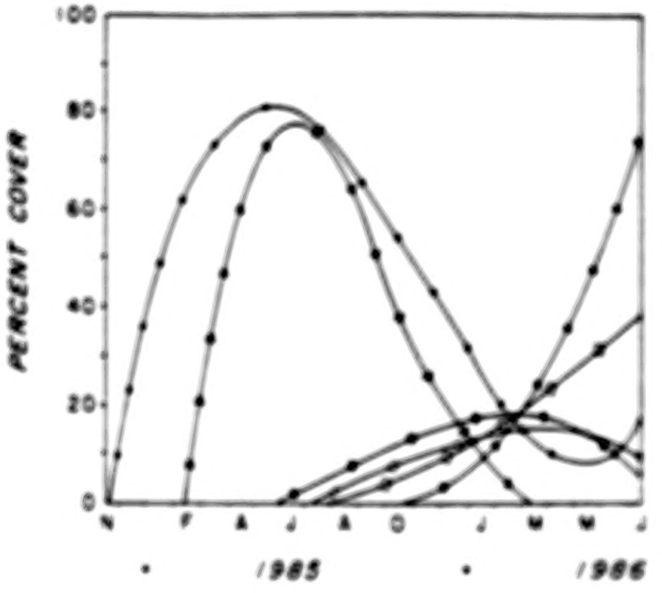


Figure I-A-2a

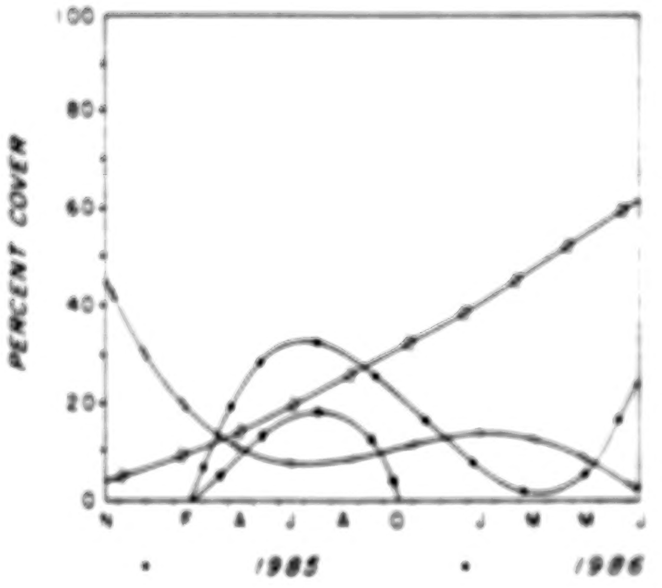


Figure I-A-2b

Figure I-A-2a,b. General successional patterns found in the centers of a) completely disturbed and b) partially disturbed 50 x 50 cm plots. Lines were generated with the help of best fit third order polynomials through percent cover data points collected only on the months indicated; see Figures I-A-4a through I-A-4g and Figures I-A-5a through I-A-5e for details on actual values.

Table I-A-3. List of species that colonized completely cleared and partially cleared plots.

Plants	*Alaria marginata*
	Analipus japonicus
	Bossiella plumosa
	Calliarthron tuberculosum
	Callithamnion pikeanum
	Ceramium pacificum
	Cladophora columbiana
	Colpomenia sinuosa
	Corallina officinalis
	Corallina vancouveriensis
	Cylindrocarpus rugosus
	Diatoms, benthic
	Egregia menziesii
	Endocladia muricata
	Gigartina canaliculata
	Gigartina exasperata
	Iridaea flaccida
	Lomentaria sp.[1]
	Mastocarpus papillatus (*Gigartina papillata*)
	Microcladia borealis
	Pelvetia fastigiata
	Petalonia fascia
	Petrocelis franciscana
	Polysiphonia hendryi
	Porphyra perforata
	Ralfsia pacifica
	Rhodoglossum affine
	Scytosiphon lomentaria
	Spongomorpha coalita
	Ulva californica
	Ulva lactuca
	Ulva lobata
Sessile and Motile Animals	*Anthopleura elegantissima*
	Balanus glandula
	Chthamalus spp.
	Mytilus californianus
	Pollicipes polymerus
	Tetraclita rubescens
	Strongylocentrotus purpuratus

---

[1] Undescribed.

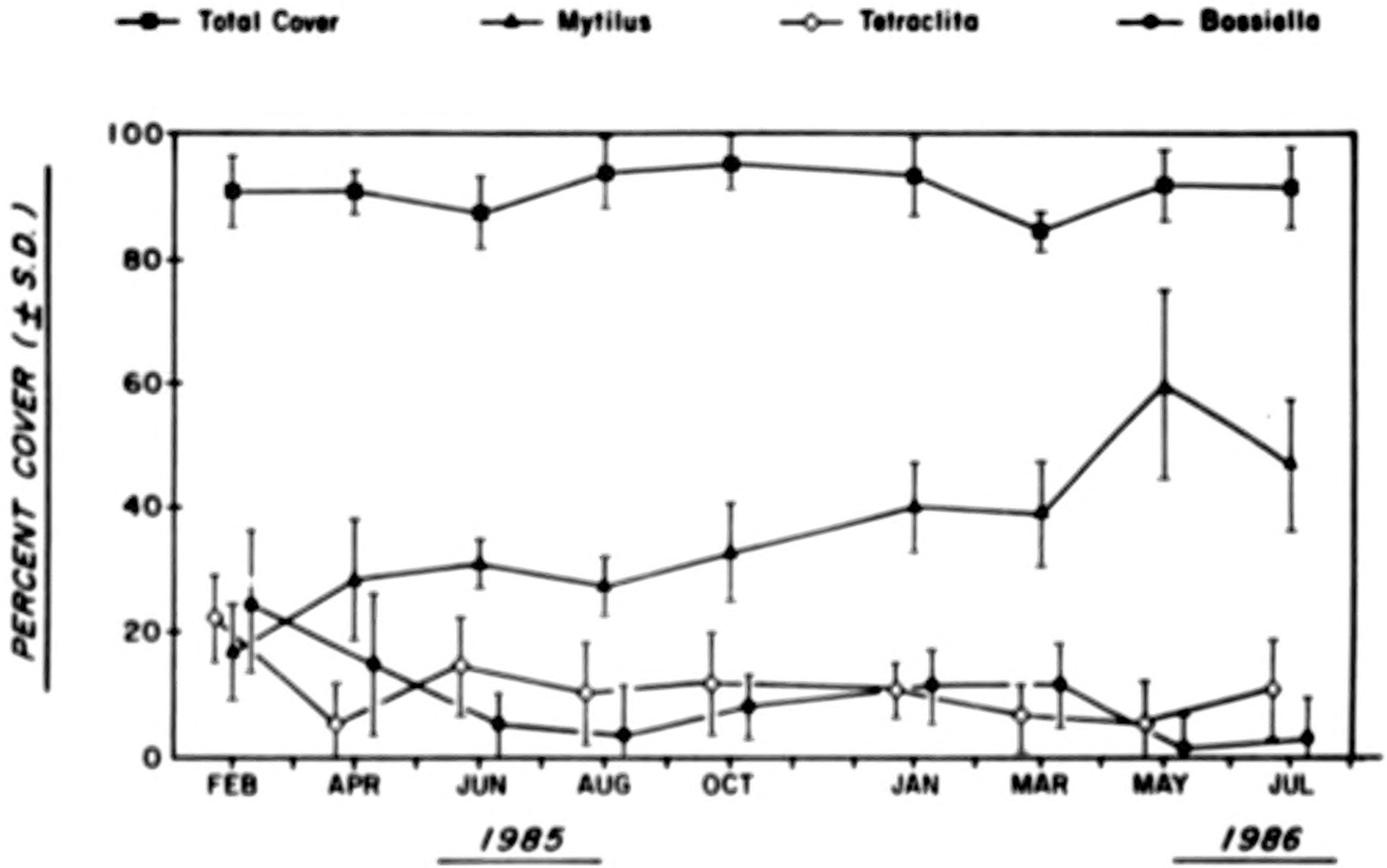


Figure I-A-3. Mean percent cover (± SD, n=12), through time of common organisms in control plots.

Table I-A-4. Sessile organisms found in control plots.

Abundance Category[1]	Species[2]	
ABUNDANT	*_Mytilus californianus_	
	*_Tetraclita rubescens_	
	Bossiella plumosa[1]	
	Ulva spp.[2]	
	Bare Rock	
COMMON	*_Balanus glandula_	
	Analipus japonicus	
	*_Pollicipes polymerus_	
PRESENT	_Cladophora columbiana_	_Porphyra perforata_
	Pelvetia fastigiata	"Petrocelis"[3]
	*_Chthamalus_ spp.	_Endocladia muricata_
	Mastocarpus papillatus	
RARE	_Ralfsia pacifica_	_Iridaea flaccida_[4]
	Ceramium californicum	_Cylindrocarpus rugosus_
	Corallina officinalis	_Colpomenia_ sp.
	Corallina vancouveriensis	*_Anthopleura elegantissima_
	Diatoms, benthic	

1. _Bossiella plumosa_ was combined with pink crust % cover.
2. Mostly _Ulva lobata_.
3. Sporangial stage of _Mastocarpus_.
4. Has been suggested to be conspecific to _I. cordata_ (Foster, 1982).

---

[1] Abundance categories were determined from maximum percent cover attained during the experimental period: abundant (>15%), common (5-15%), present (1-5%), and rare (<1%).

[2] Within each category, organisms are ranked from most to least abundant from top to bottom and left to right.

* Denotes animal species. Unmarked species are algae.

With the succession patterns described above providing a framework for comparison, the following sections will consider details of individual species in different plot sizes and positions within plots.

Species Cover in Complete Disturbances - Effects of Size and Position

During succession the combined cover of all species increased rapidly but was lower in the borders than in the centers of patches, especially early in succession (Figure I-A-4a). This difference between borders and centers was statistically significant for the first eight months of the study (Table I-A-5). Size, on the other hand, did not have an effect on total cover, except at the smallest level (10 x 10 cm patches; Table I-A-5). Statistical tests could only be performed between the three largest sizes because the smallest size could not be subsampled and has, by definition, no center (Table I-A-2). Total cover in 10 x 10 cm patches was negligible for the first nine months and remained relatively low throughout the study (Figure I-A-4a).

Ulva sp(p). was abundant as an early colonist but then declined in cover (Figure I-A-4b). It was significantly less abundant in the borders than in the centers of patches for the first seven months (Figure I-A-4b, Table I-A-5). This edge effect became less pronounced through time for all plot sizes. Like total cover, there was no significant size effect between the three larger patch sizes. The 10 x 10 cm patch did not contain *Ulva* until six months after it was found in other plots.

Though *Porphyra perforata* (Figure I-A-4c) showed the same bloom-decline pattern as *Ulva*, there was no significant difference in its percent cover between centers and borders (Table I-A-5). Plot size did not affect *P. perforata* abundance except in the 10 x 10 cm patch size. *P. perforata* did not grow in the smallest patches except for a brief appearance in August 1985. In September, the summer fog in Monterey becomes less frequent and the coincidence of this with winds and low tides creates a drying environment that may have caused the rapid decline of *P. perforata*. Because *P. perforata* and *Ulva* were abundant at the same time, layering of these species was common. *P. perforata* almost invariably formed the top layer, perhaps aiding *Ulva* through the months of September and October by keeping it moist.

Egregia menziesii, a mid-successional species, was highly variable in its cover and was less abundant than the species discussed above (note scale in Figure I-A-4d). Though a trend might suggest edge effects, these are not statistically significant (Table I-A-5). Size, again, was only important at the smallest plot size level; *E. menziesii* was never found in the smallest patches. This large brown alga was found in patches on the study site but was more common at lower tide levels in moderate surge. *E. menziesii* can tolerate winter swells, and its decline in early spring may have resulted from the lack of wave spray during low tides.

Iridaea flaccida was also a later successional species and the first discussed so far that was not declining at the end of year 2 of this five-year study. In March and May of 1986 there was a statistically significant edge effect, but by July it was only a trend (Figure I-A-4e, Table I-A-5). *Iridaea flaccida* was never found in the smallest patches but was found in similar amounts in the patches of other sizes.

Finally, *Bossiella plumosa* (Figure I-A-4f) is a species found in well-developed communities at this site (Figure I-A-3). It showed no significant edge effect (Table I-A-

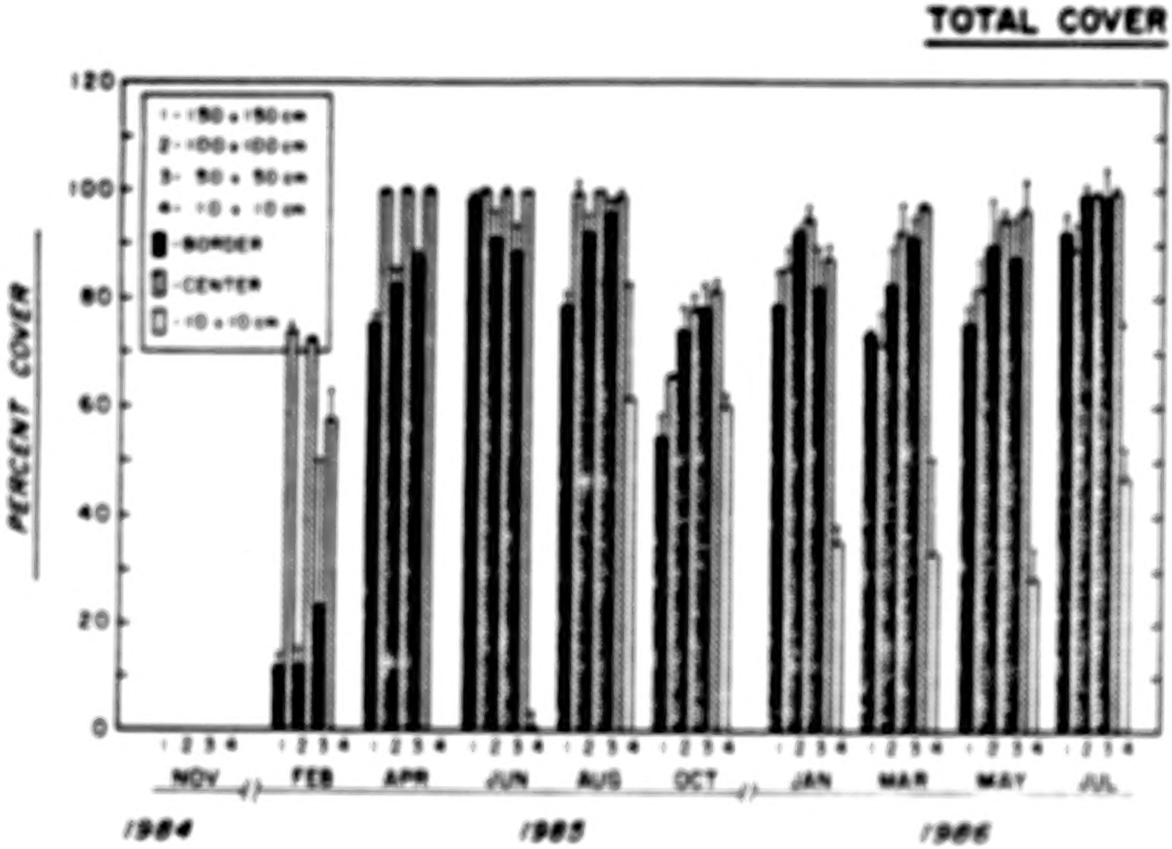


Figure I-A-4a. Percent cover [±1 SD of replicate plots (n=4), calculated by combining subsamples] through time of total cover in different sized plots, and in different positions within completely cleared plots.

The plot sizes are indicated at the base of each histogram: 1 = 150 x 150 cm, 2 = 100 x 100 cm, 3 = 50 x 50 cm and 4 = 10 x 10 cm. Within each plot size, percent cover in borders and centers is indicated: the region extending 10 cm from the edge of a plot is considered the border therefore 10 x 10 cm plots have no centers.

Ulva

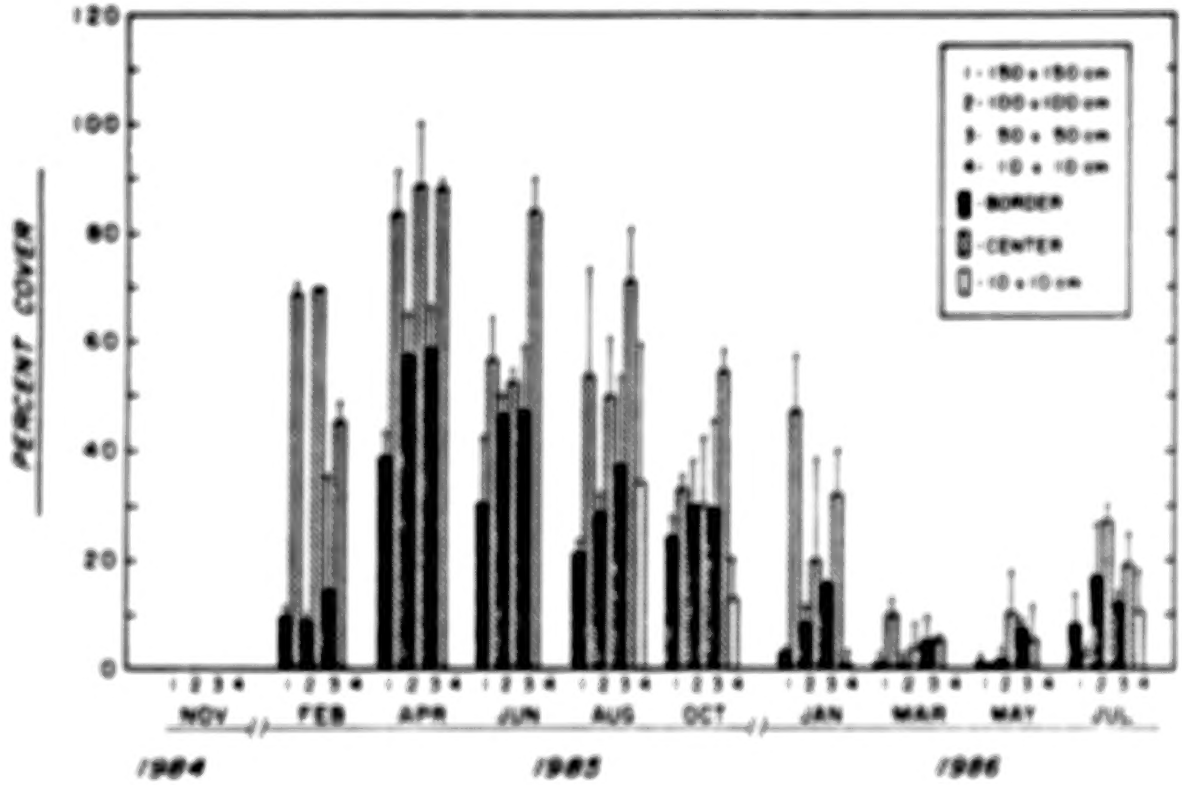


Figure I-A-4b. Percent cover [±1 SD of replicate plots (n=4), calculated by combining subsamples] through time of *Ulva sp(p)*. in different sized plots, and in different positions within completely cleared plots.

The plot sizes are indicated at the base of each histogram: 1 = 150 x 150 cm, 2 = 100 x 100 cm, 3 = 50 x 50 cm and 4 = 10 x 10 cm. Within each plot size, percent cover in borders and centers is indicated: the region extending 10 cm from the edge of a plot is considered the border therefore 10 x 10 cm plots have no centers.

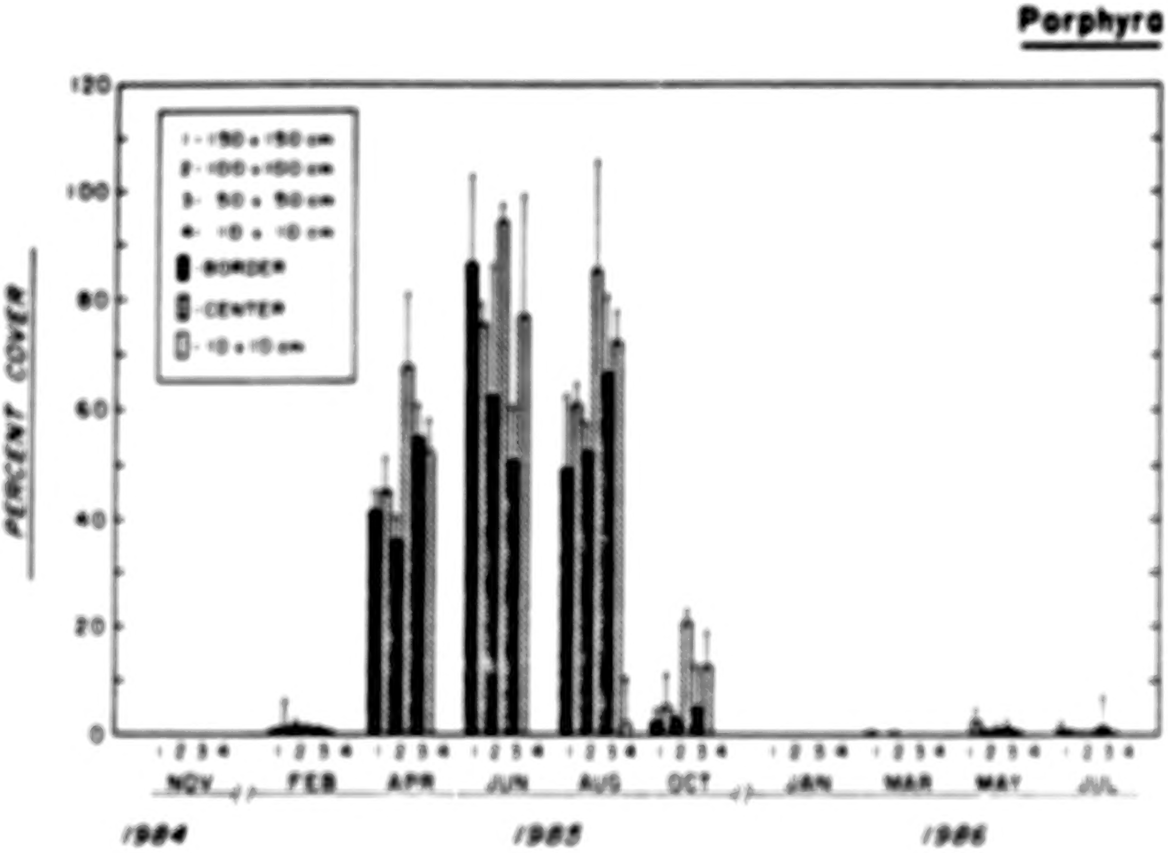


Figure 1-A-4c. Percent cover [±1 SD of replicate plots (n=4), calculated by combining subsamples] through time of *Porphyra perforata* in different sized plots, and in different positions within completely cleared plots.

The plot sizes are indicated at the base of each histogram: 1 = 150 x 150 cm, 2 = 100 x 100 cm, 3 = 50 x 50 cm and 4 = 10 x 10 cm. Within each plot size, percent cover in borders and centers is indicated: the region extending 10 cm from the edge of a plot is considered the border therefore 10 x 10 cm plots have no centers.

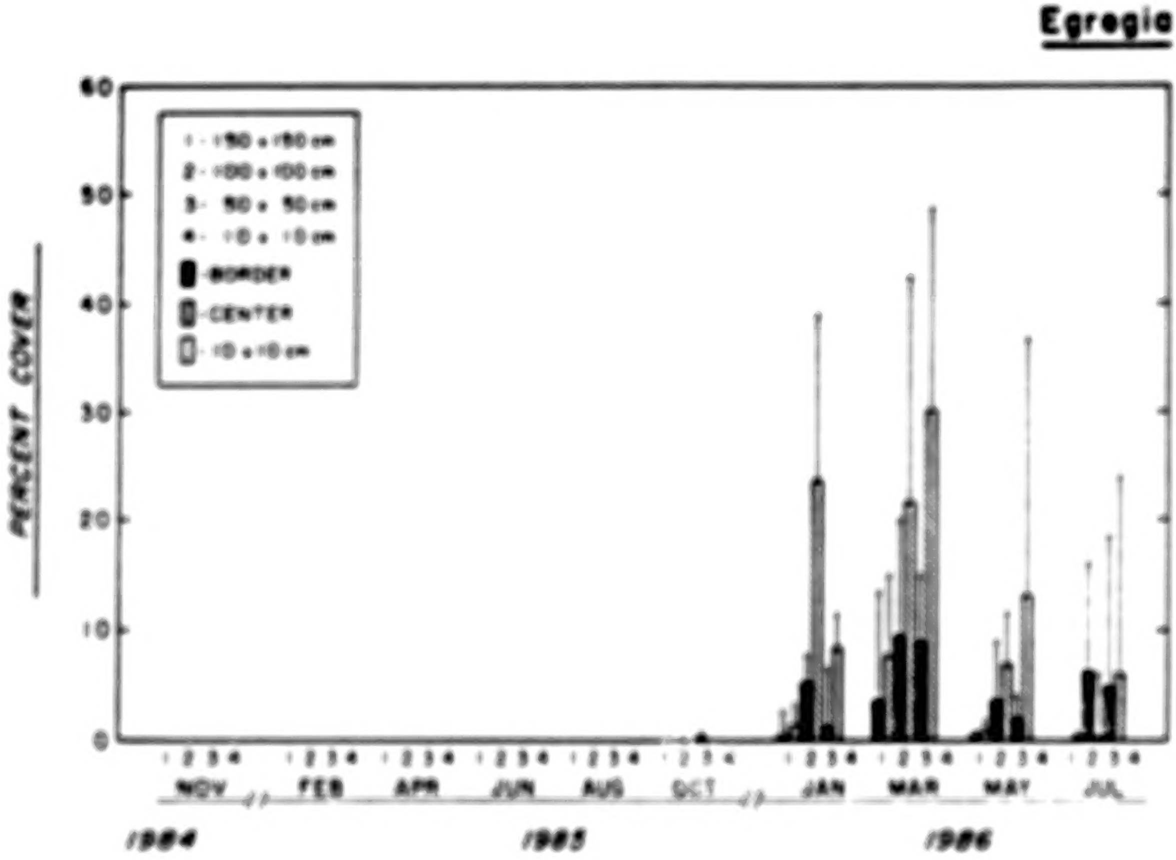


Figure I-A-4d. Percent cover [±1 SD of replicate plots (n=4), calculated by combining subsamples] through time of *Egregia menziesii* in different sized plots, and in different positions within completely cleared plots.

The plot sizes are indicated at the base of each histogram: 1 = 150 x 150 cm, 2 = 100 x 100 cm, 3 = 50 x 50 cm and 4 = 10 x 10 cm. Within each plot size, percent cover in borders and centers is indicated: the region extending 10 cm from the edge of a plot is considered the border therefore 10 x 10 cm plots have no centers.

Iridaea

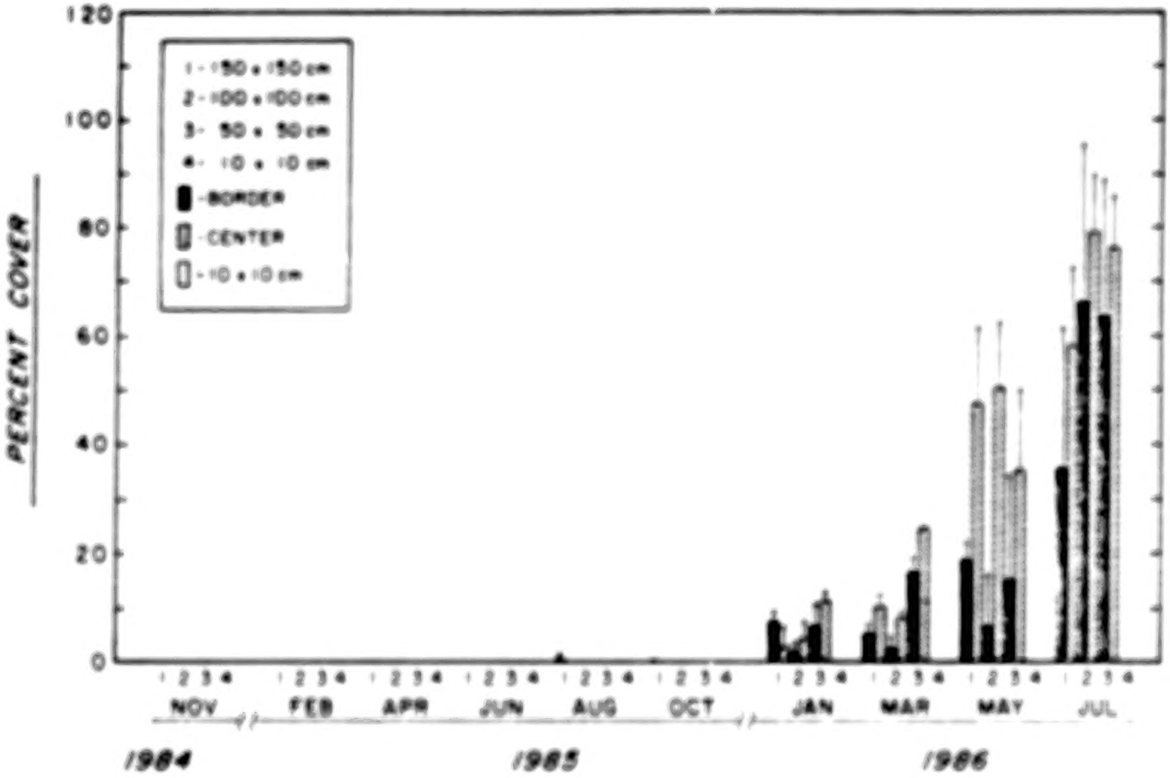


Figure I-A-4e. Percent cover [±1 SD of replicate plots (n=4), calculated by combining subsamples] through time of *Iridaea flaccida* in different sized plots, and in different positions within completely cleared plots.

The plot sizes are indicated at the base of each histogram: 1 = 150 x 150 cm, 2 = 100 x 100 cm, 3 = 50 x 50 cm and 4 = 10 x 10 cm. Within each plot size, percent cover in borders and centers is indicated: the region extending 10 cm from the edge of a plot is considered the border therefore 10 x 10 cm plots have no centers.

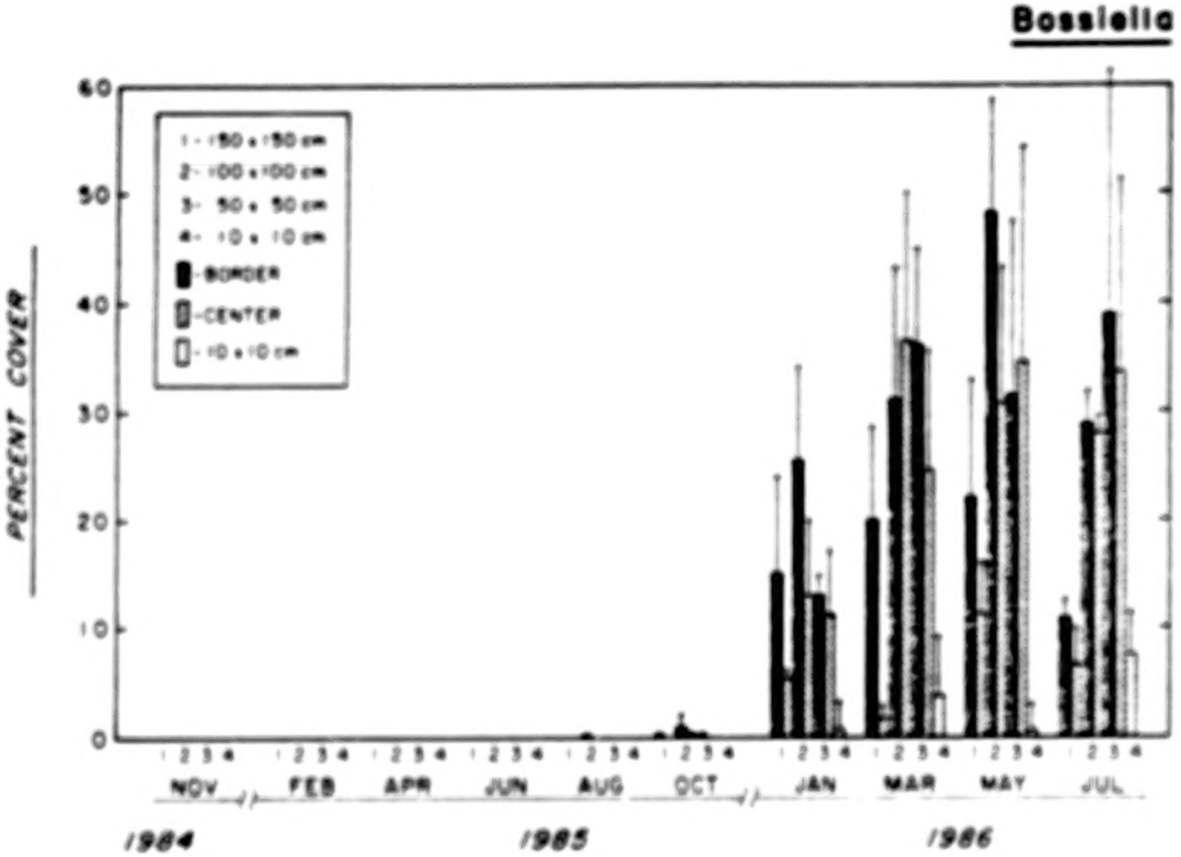


Figure I-A-4f. Percent cover [±1 SD of replicate plots (n=4), calculated by combining subsamples] through time of *Bossiella plumosa* in different sized plots, and in different positions within completely cleared plots.

The plot sizes are indicated at the base of each histogram: 1 = 150 x 150 cm, 2 = 100 x 100 cm, 3 = 50 x 50 cm and 4 = 10 x 10 cm. Within each plot size, percent cover in borders and centers is indicated: the region extending 10 cm from the edge of a plot is considered the border therefore 10 x 10 cm plots have no centers.

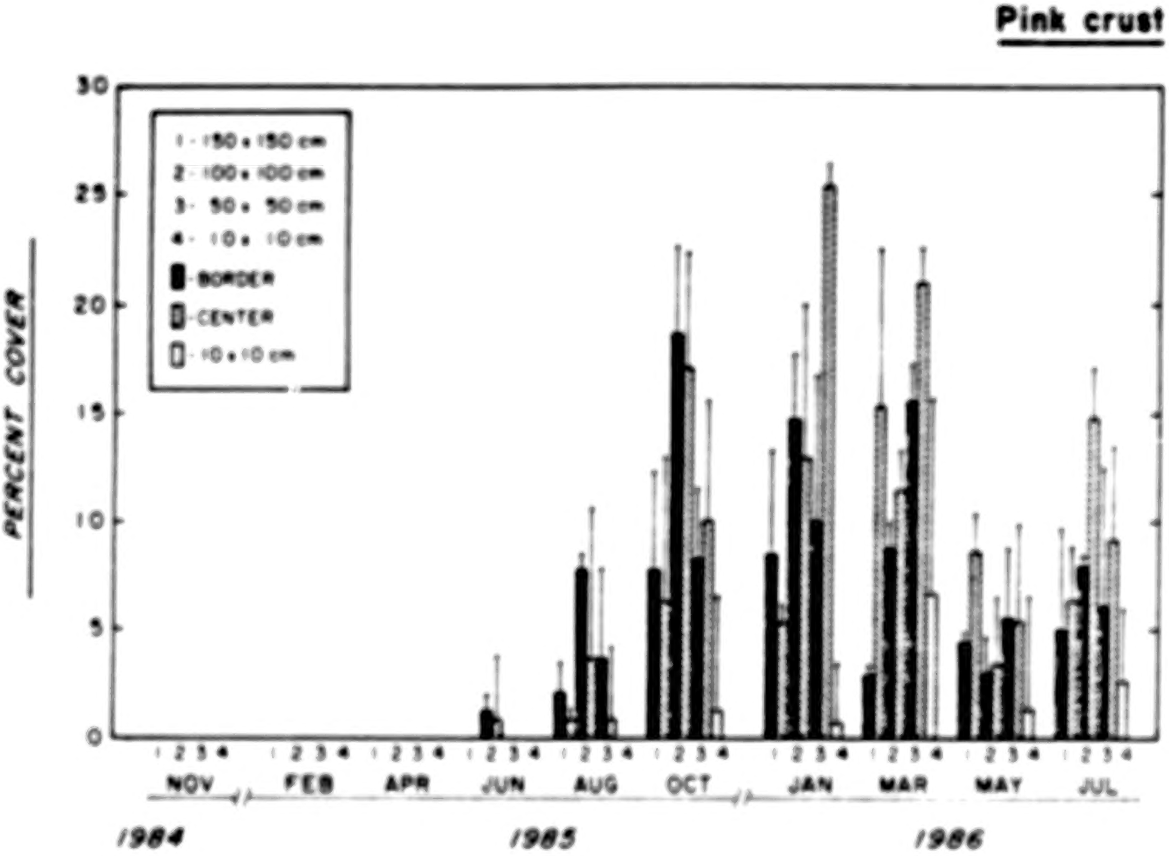


Figure I-A-4g. Percent cover [±1 SD of replicate plots (n=4), calculated by combining subsamples] through time of pink crusts in different sized plots, and in different positions within completely cleared plots.

The plot sizes are indicated at the base of each histogram: 1 = 150 x 150 cm, 2 = 100 x 100 cm, 3 = 50 x 50 cm and 4 = 10 x 10 cm. Within each plot size, percent cover in borders and centers is indicated: the region extending 10 cm from the edge of a plot is considered the border therefore 10 x 10 cm plots have no centers.

Table I-A-5. Results of analyses of variance[1] on the effects of plot size, position (= Pos.) within plot (border vs. center) and replicate plots on species abundance through time in completely disturbed plots.[2] Heteroscedasticity was found when one or more groups of sub-samples had a variance of zero.

	February 1985					April 1985					June 1985				
Species	Size	Plot Within Size	Pos.	Size X Pos.	Plot Within Size X Pos.	Size	Plot Within Size	Pos.	Size X Pos.	Plot Within Size X Pos.	Size	Plot Within Size	Pos.	Size X Pos.	Plot Within Size X Pos.
Ulva	*n.s.	p<.01	p<.001	n.s.	n.s.	*n.s.	p<.05	p<.01	n.s.	n.s.	n.s.	p<.05	p<.05	n.s.	n.s.
Porphyra	⊙	⊙	⊙	⊙	⊙	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	p<.02	n.s.	n.s.	n.s.
Egregia	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙
Iridaea	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙
Bossiella	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙	⊙
Total Cover	n.s.	p<.001	p<.001	n.s.	n.s.	*n.s.	n.s.	p<.001	n.s.	n.s.	*n.s.	n.s.	p<.05	n.s.	n.s.

Table I-8-5. (Continued)

	August 1985					October 1985					January 1986				
Species	Size	Plot Within Size	Pos.	Size X Pos.	Plot Within Size X Pos.	Size	Plot Within Size	Pos.	Size X Pos.	Plot Within Size X Pos.	Size	Plot Within Size	Pos.	Size X Pos.	Plot Within Size X Pos.
Ulva	n.s.	p<.02	n.s	n.s.	n.s.	n.s.	p<.001	n.s	n.s.	n.s.	[a]n.s.	p<.001	p<.05	n.s.	p<.05
Porphyra	n.s	p<.01	n.s.	n.s.	n.s.	n.s.	p<.05	n.s.	n.s.	n.s.	0	0	0	0	0
Egregia	0	0	0	0	0	0	0	0	0	0	[a]n.s.	p<.01	n.s.	n.s.	n.s.
Iridaea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bossiella	0	0	0	0	0	0	0	0	0	0	n.s.	n.s.	n.s.	n.s.	n.s.
Total Cover	[a]n.s.	n.s.	p<.01	n.s.	n.s.	n.s.	p<.05	n.s.	n.s.	n.s.	n.s.	p<.01	n.s.	n.s.	n.s.

Table I-4-5. (Continued)

	March 1986					May 1986					July 1986				
Species	Site	Plot Within Site	Pos.	Site X Pos.	Plot Within Site X Pos.	Site	Plot Within Site	Pos.	Site X Pos.	Plot Within Site X Pos.	Site	Plot Within Site	Pos.	Site X Pos.	Plot Within Site X Pos.
Ulva	o	o	o	o	o	o	o	o	o	o	n.s.	p<.05	n.s.	n.s.	n.s.
Porphyra	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Egregia	*n.s.	p<.0001	n.s.	n.s.	n.s.	o	o	o	o	o	o	o	o	o	o
Iridaea	*n.s.	n.s.	p<.02	n.s.	n.s.	n.s.	p<.0001	p<.0007	n.s.	n.s.	n.s.	p<.0001	n.s.	n.s.	n.s.
Bossiella	n.s.	p<.0001	n.s.	n.s.	n.s.	n.s.	p<.0001	n.s.	n.s.	p<.05	n.s.	p<.0001	n.s.	n.s.	n.s.
Total Cover	n.s.	p<.01	n.s.	n.s.	n.s.	n.s.	p<.01	n.s.	n.s.	n.s.	*n.s.	p<.01	n.s.	n.s.	n.s.

[1] See Appendix A-1 for ANOVA model used.

[2] All tests were evaluated as two-tailed with = 0.05. n.s. (no significant difference), p (appropriate p value) or o (not enough data to perform the test: abundance not > 75% in at least one replicate plot) is indicated for each test result.

* F max test determined unequal variances.

5) but again the 10 x 10 cm patches had distinctly less cover than the larger sizes. Pink crusts (Figure I-A-4g) were probably the basal portion of *B. plumosa*, as suggested by their decline as *B. plumosa* uprights developed, but as mentioned earlier, these crusts could constitute groups of several species. Pink crusts do show the same trends in size and position effects as *B. plumosa*.

Differences Between Replicate Plots and Spore Dispersal Distances

Although statistically significant differences in cover were not found between the three larger size plots, all individual species showed differences between replicate plots at some time during the study (Table I-A-5). Subsampling allows for this test, and the high degrees of freedom in the analyses make the test sensitive to the natural variability in this community. Possible causes of this variability between plots are slight differences in wave exposure or tidal heights, or different locations with respect to spore sources. Variability may also be associated with the size of each organism relative to the sample quadrat (Andrew and Mapstone, 1987); in this case, constraints were imposed by natural patch sizes and a design that allows statistical comparisons of plot sizes.

If the species considered had limited spore dispersal, they would be under-represented in the centers of large plots. This pattern would result in a size x position interaction in the analysis of variance. This was not the case (Table I-A-5), suggesting that the algae considered were not dispersal-limited at the scale of 1.5-m clearings. Shortest distance measurements from recruits to conspecific adults confirmed this. Though no statistical test was performed, it was noted that there were more *Egregia menziesii* in experimental patches closer to a large conspecific bed next to the study site. *E. menziesii* might be limited on the order of 5 m, and this may have been one cause for the high variability seen in Figure I-A-4d. Other studies have suggested that local parental stocks of some intertidal algae are necessary for (Dayton, 1973) or may enhance (Sousa, 1984b) patch recruitment.

Effects of Position in Partial Disturbances

In contrast to the completely disturbed plots, there were no dramatic differences in growth between edges and centers in partially disturbed plots. Though there is a slight general trend of lower abundances in the borders than in the centers of patches (Figures I-A-5a-e), it is only statistically significant on one sampling date for *Ulva* sp(p). and on two occasions for total cover (Table I-A-6).

Complete Versus Partial Disturbances

The effects of disturbance severity on succession are demonstrated in the comparison of 50 x 50 cm partial and complete disturbances shown in Figures I-A-5a-e and in Table I-A-6. The first obvious difference is that *Iridaea flaccida* and *Egregia menziesii*, the prominent mid-successional species in complete disturbances, were essentially absent from partial disturbances (maximum percent cover: *I. flaccida* = 0.15, *E. menziesii* = 0.07; Figure I-A-3). Foster (1982) found that *I. flaccida* recruitment was completely inhibited by algal crusts and holdfasts, while adjacent completely cleared plots had high recruitment.

Ulva and *Porphyra* were initially significantly lower in abundance in partial disturbances (November-April, $p<0.02$, Table I-A-6). This trend continued until their

TOTAL COVER

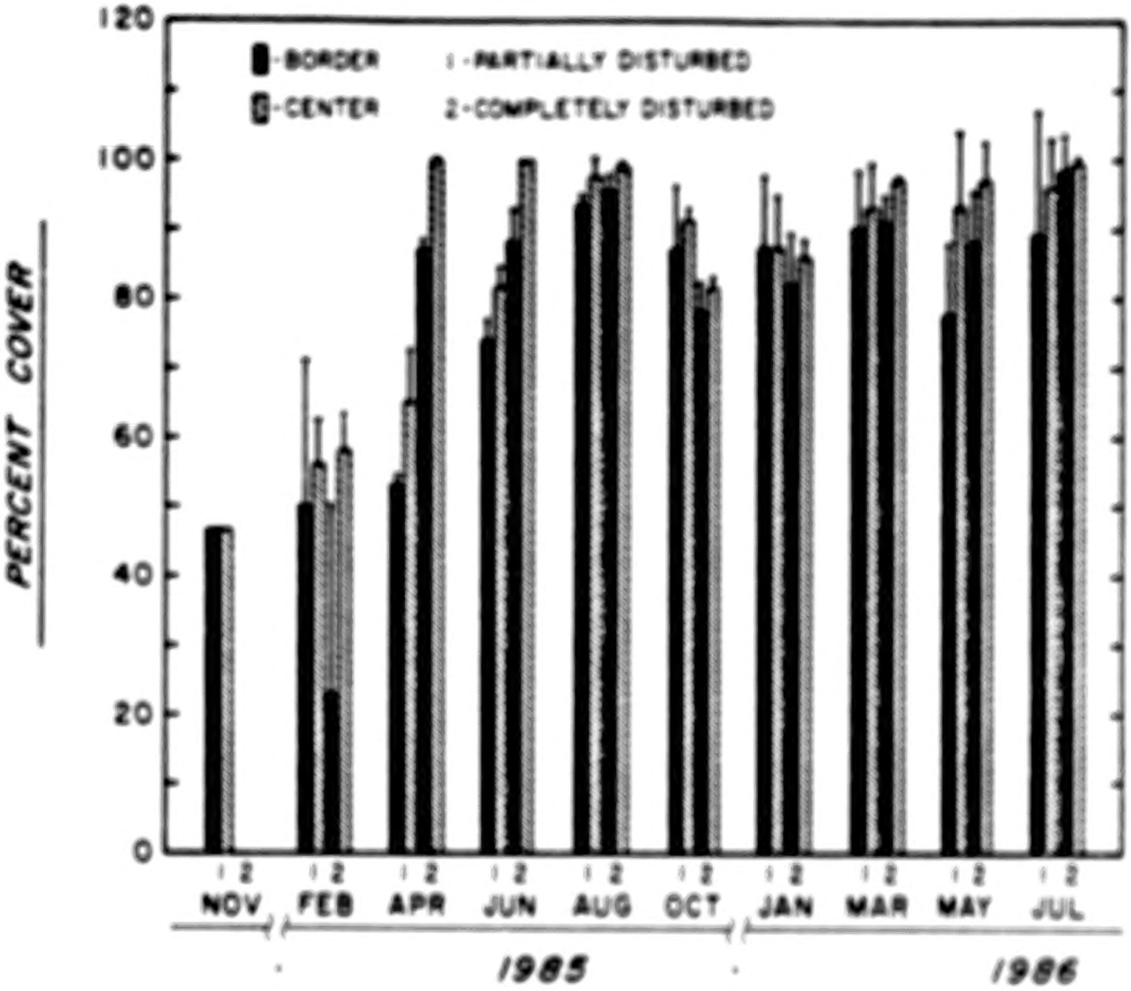
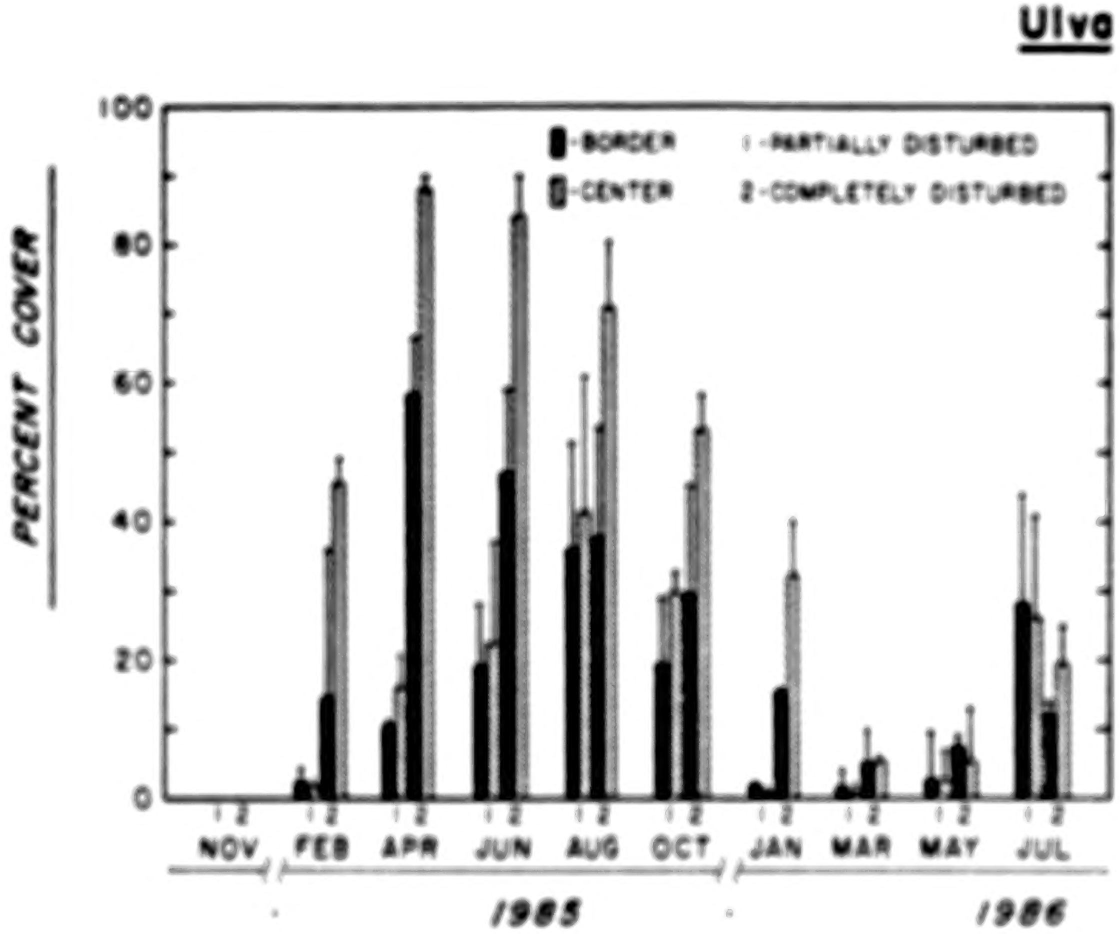


Figure 1-A-5a. Percent cover [±1 SD of replicate plots (n=4), calculated by combining subsamples] through time of total cover in completely versus partially disturbed 50 x 50 cm plots, and differences between positions within each plot type.

The plot types are indicated at the base of each histogram: 1 = partially disturbed and 2 = completely disturbed. Within each plot type, percent cover in borders and centers is indicated.



Ulva

Figure I-A-5b. Percent cover [±1 SD of replicate plots (n=4), calculated by combining subsamples] through time of *Ulva* sp(*p*). in completely versus partially disturbed 50 x 50 cm plots, and differences between positions within each plot type.

The plot types are indicated at the base of each histogram: 1 = partially disturbed and 2 = completely disturbed. Within each plot type, percent cover in borders and centers is indicated.

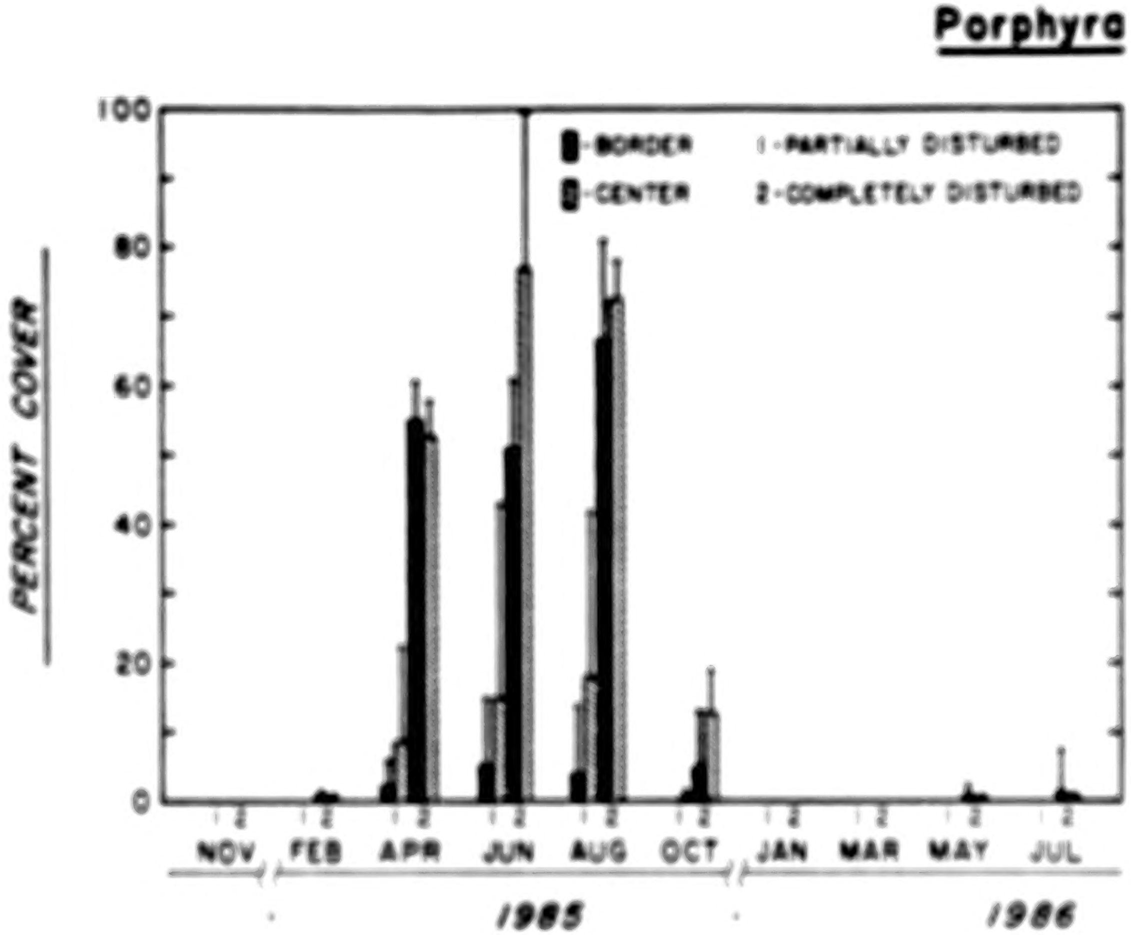
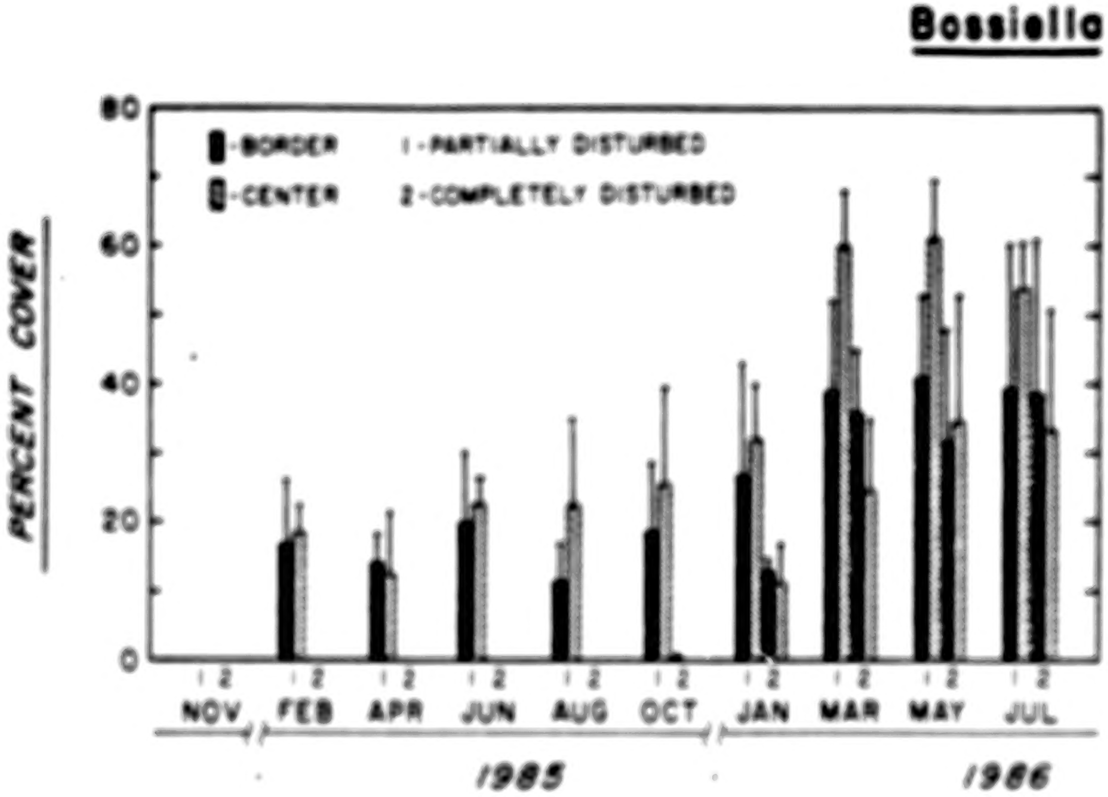


__Figure I-A-5c.__ Percent cover [±1 SD of replicate plots (n=4), calculated by combining subsamples] through time of *Porphyra perforata* in completely versus partially disturbed 50 x 50 cm plots, and differences between positions within each plot type.

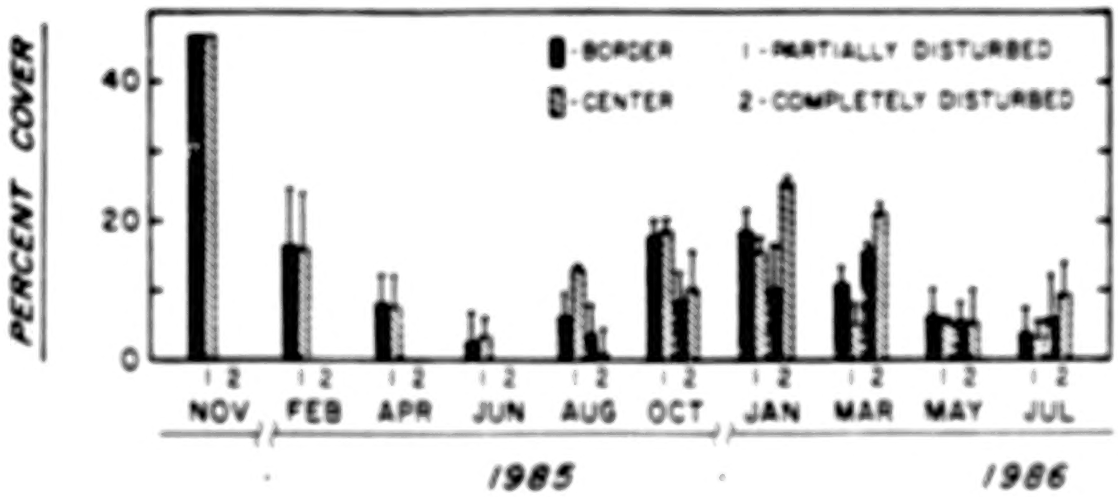
The plot types are indicated at the base of each histogram: 1 = partially disturbed and 2 = completely disturbed. Within each plot type, percent cover in borders and centers is indicated.



Bossiella

Figure I-A-5d. Percent cover [±1 SD of replicate plots (n=4), calculated by combining subsamples] through time of *Bossiella plumosa* in completely versus partially disturbed 50 x 50 cm plots, and differences between positions within each plot type.

The plot types are indicated at the base of each histogram: 1 = partially disturbed and 2 = completely disturbed. Within each plot type, percent cover in borders and centers is indicated.



Pink crust

Figure I-A-5e. Percent cover [±1 SD of replicate plots (n=4), calculated by combining subsamples] through time of pink crusts in completely versus partially disturbed 50 x 50 cm plots, and differences between positions within each plot type.

The plot types are indicated at the base of each histogram: 1 = partially disturbed and 2 = completely disturbed. Within each plot type, percent cover in borders and centers is indicated.

Table 1-4-6. Results of analyses of variance[1] on the effects of disturbance severity, position within plot (border vs center) and replicate plots on species abundance through time.[2]

	February 1985					April 1985					June 1985				
Species	Severity	Plot Within Severity	Pos.	Severity X Pos.	Plot Within Severity X Pos.	Severity	Plot Within Severity	Pos.	Severity X Pos.	Plot Within Severity X Pos.	Severity	Plot Within Severity	Pos.	Severity X Pos.	Plot Within Severity X Pos.
Ulva	*p<.05	p<.0004	n.s.	n.s.	n.s.	p<.01	n.s.	p<.05	n.s.	n.s.	n.s.	p<.02	n.s.	n.s.	n.s.
Porphyra	0	0	0	0	0	*p<.02	n.s.	n.s.	n.s.	n.s.	*n.s.	p<.002	n.s.	n.s.	n.s.
Egregia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Iridaea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bossiella	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Total Cover	n.s.	p<.0004	n.s.	n.s.	p<.02	*p<.01	n.s.	p<.05	n.s.	n.s.	*p<.01	n.s.	n.s.	n.s.	n.s.

Table I-A-4. (Continued)

	August 1985					October 1985					January 1986				
Species	Sever-ity	Plot Within Sever-ity	Pos.	Sever-ity X Pos.	Plot Within Sever-ity X Pos.	Sever-ity	Plot Within Sever-ity	Pos.	Sever-ity X Pos.	Plot Within Sever-ity X Pos.	Sever-ity	Plot Within Sever-ity	Pos.	Sever-ity X Pos.	Plot Within Sever-ity X Pos.
Ulva	n.s.	p<.0001	n.s.	n.s.	n.s.	n.s.	p<.0002	n.s.	n.s.	n.s.	*p<.01	n.s.	n.s.	n.s.	n.s.
Porphyra	*n.s.	p<.0002	n.s.	n.s.	n.s.	*n.s.	p<.01	n.s.	n.s.	n.s.	0	0	0	0	0
Egregia	0	0	0	0	0	0	0	0	0	0	X	X	X	X	X
Iridaea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bossiella	X	X	X	X	X	X	X	X	X	X	n.s.	p<.01	n.s.	n.s.	n.s.
Total Cover	*n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	p<.05	n.s.	n.s.	n.s.	n.s.	p<.0007	n.s.	n.s.	n.s.

Table 4-4-6. (Continued)

	March 1990					May 1990					July 1990				
Species	Severity	Plot Within Severity	Pos.	Severity X Pos.	Plot Within Severity X Pos.	Severity	Plot Within Severity	Pos.	Severity X Pos.	Plot Within Severity X Pos.	Severity	Plot Within Severity	Pos.	Severity X Pos.	Plot Within Severity X Pos.
Ulva	o	o	o	o	o	o	o	o	o	o	n.s.	p=.01	n.s.	n.s.	n.s.
Porphyra	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Egregia	A	A	A	A	A	o	o	o	o	o	o	o	o	o	o
Iridaea	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
Bossiella	n.s.	p=.0029	n.s.	n.s.	n.s.	n.s.	p=.0008	n.s.	n.s.	n.s.	n.s.	p=.0001	n.s.	n.s.	n.s.
Total Cover	^a^n.s.	p=.0002	n.s.	n.s.	n.s.	^a^n.s.	p=.0002	p=.04	n.s.	n.s.	^a^n.s.	p=.0001	n.s.	n.s.	n.s.

[1] See Appendix B-2 for ANOVA model used.

[2] All tests were evaluated as two-tailed with 0.05. A (the species in question was absent from one of the severity levels, and no test was performed), n.s. (no significant difference), p (appropriate p value) or o (not enough data to perform the test: abundance not > 15% in at least one replicate plot) is indicated for each test result. Heteroscedasticity was found when one or more groups of sub-samples had a variance of zero.

[a] F max test determined unequal variances.

demise as early successional species (Figures I-A-5b, c). By June 1986, *Ulva* abundance in partially disturbed plots had reached parity with that of completely disturbed plots.

Bossiella plumosa quickly recovered from the remaining crusts so it was initially abundant in the partial disturbances and absent in the complete disturbances (Figure I-A-5d). Not surprisingly, the pink crust category (Figure I-A-5e) showed the same initial pattern until much of it developed into upright *Bossiella* fronds. Like *Ulva* and *Porphyra*, the abundance of *B. plumosa* in the partially disturbed plots was similar to the completely disturbed plots by the end of the study. Total cover was initially higher in the partial disturbances, reflecting the presence of algal crusts. This difference was no longer statistically significant as *Ulva* and *Porphyra* became abundant in completely disturbed plots, and reversed before the uniform high algal cover developed after nine months.

Grazer Abundance

After molluscan grazers were counted, all combinations of grazer species and size were graphed to look for trends correlated with edge effects (Figures I-A-6a, b; I-A-7, I-A-8). The limpet grazers found on one sampling date in February 1985 were ($N=27$): 50 percent *"Collisella" scabra*, 31 percent *Lottia pelta*, 19 percent other species of limpets (*Lottia digitalis*, *Lottia gigantea*, other *Lottia* species, or too small to identify). Greater than 99 percent of the chitons ($N=166$) were *Nuttallina californica*. Amphipods were sometimes found in high densities in shallow pools, but an alternate sample was taken if sample quadrats fell in these locations. For the first eight months, a trend of higher chiton densities in the small 10 x 10 cm plots and borders was found when compared to the centers of plots (Figure I-A-6a). Similar trends were not found for limpets (Figure I-A-6b). Partially disturbed plots, which in general showed no edge effect, did not show the chiton density differences found in the completely disturbed plots (Figure I-A-7). Chiton densities in these plots were, however, higher than in the edges of completely disturbed plots and similar to densities found in control plots (February 1985, 3.1/100cm^2, S.D.$=2$). Because the above trends are only suggestive, the chiton exclusion experiment was initiated.

Chiton Exclusion Experiment

The chiton exclusion experiment began in April 1986 and continued for six months. Fences excluding grazers will be referred to as the experimental treatment and the fences including chitons will be referred to as the control. The fences were effective at keeping molluscan grazers out, but periodically a chiton would leave the enclosures (possibly by detachment and drifting, or from predation). After 13 days, two chitons had to be added to each control. After 45 days, one of the control fences broke and that treatment was excluded from calculations, also one and two chitons were added to the other controls. After three months, one limpet was removed from a control. After five months, limpet recruits had to be removed from the controls and one of the experimental treatment fences broke. Finally, by November 1986 the experiment was discontinued because grazers invaded the experimental treatments.

The effect of *Nuttallina californica* grazing was dramatic (Figure I-A-8). The percent cover of diatoms and *Ulva* reached 100 percent in the absence of *Nuttallina californica* and was maintained at less than 30 percent in the chitons' presence; these differences are statistically significant [diatoms (May) and *Ulva* (July), $p<0.01$; one-tailed t-test on arcsine-

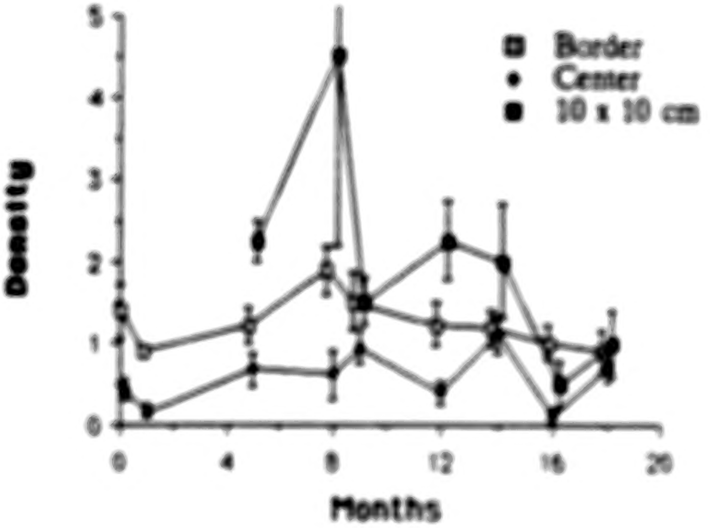


Figure I-A-6a. Mean densities (± SE, area = 100 cm², n = 4 for 10 x 10 cm or n = 18 for others) of the chiton *Nuttallina californica* (two sample periods missed for 10 x 10 cm) in different positions within completely disturbed plots through time.

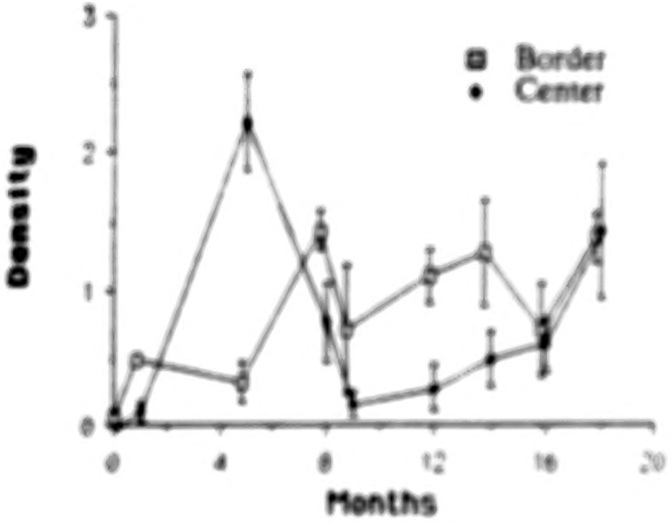


Figure I-A-6b. Mean densities (± SE, area = 100 cm², n = 4 for 10 x 10 cm or n = 18 for others) of limpets (two sample periods missed for 10 x 10 cm) in different positions within completely disturbed plots through time.

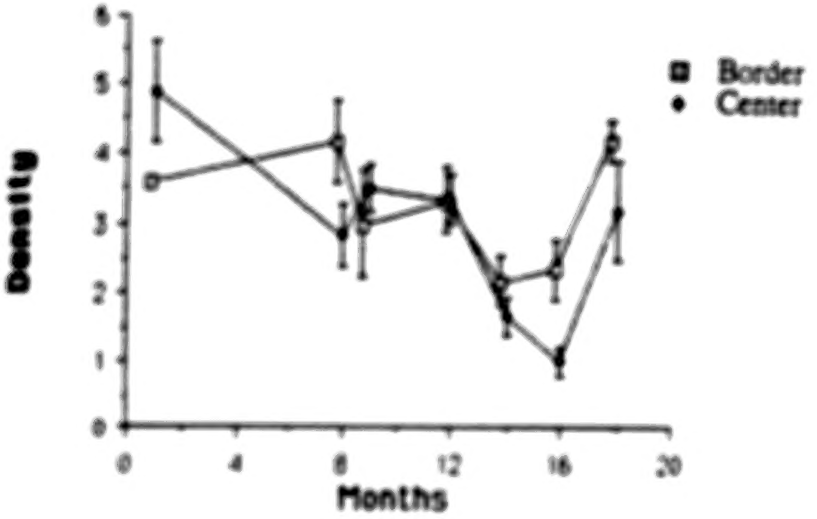


Figure I-A-7. Mean (± SE, area = 100 cm^2, n = 18) chiton *Nuttallina californica*) densities in different positions within partially cleared plots through time.

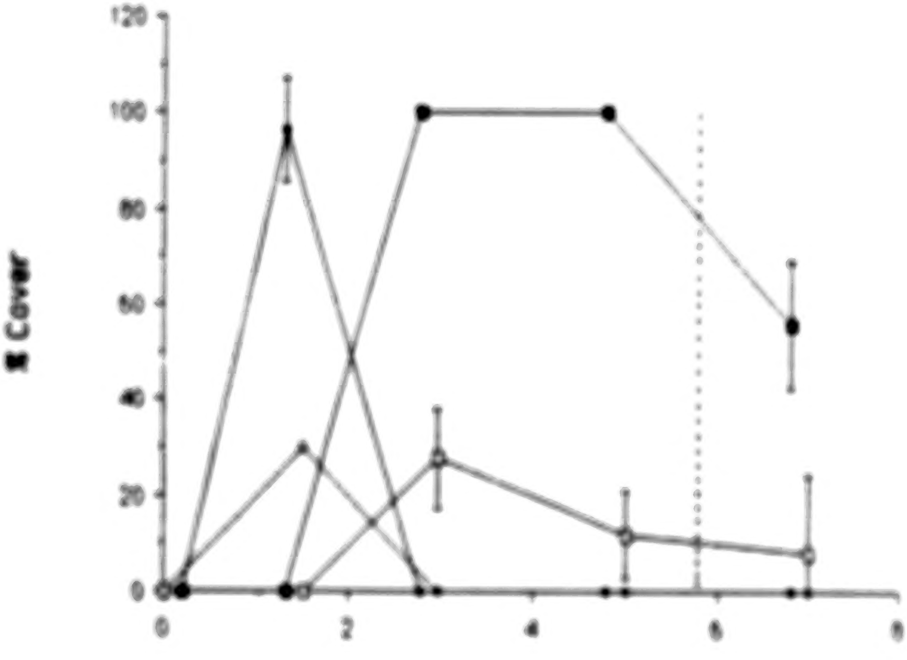


Figure I-A-8. Algal succession in the presence (open symbols) and absence (solids symbols) of chiton grazing. Diamonds = diatoms, squares = *Ulva*, dashed line = a breakdown in the experimental fences. In three instances the standard deviation was zero, so there are no error bars.

transformed data]. *Porphyra perforata* did not become abundant in the absence of grazers but after ten months, pink crusts and some fleshy algae were present in small amounts.

Barnacles were counted throughout this experiment. *Balanus glandula* made up well over half of the barnacles in each treatment, the rest being *Chthamalus* sp(p). and an occasional *Tetraclita rubescens*. Barnacle abundances were inversely proportional to algal cover. Where chiton grazing occurred, algal abundance was low and barnacle counts were high (Table I-A-7). These differences between experimental treatment and control were significant ($p<0.05$, one-tailed t-test, July). Barnacle counts in unfenced, disturbed plots were the highest (July: 183±36.5). Increased grazing by limpets made this an expected result, but the experiment was not designed to test this.

Incidental Evidence Confirming the Results of the Grazer Experiment

If a particular species is more abundant in the fence plus chiton treatment, it suggests that this species should be found in greater abundance in borders, where chitons are more abundant, than centers of patches. Though standard deviations are high and percent cover is low, this was the case for *Balanus glandula* and *Chthamalus* sp(p). (Figure I-A-9a). The brown algal crust *Cylindrocarpus rugosus* was found in both the chiton-enclosed treatments and in the 10 x 10 cm patches cleared for the main experiment (Figure I-A-9b). This suggests that *C. rugosus* is also well adapted to growth under conditions of relatively high grazing.

Table I-A-7. Effect of *Nuttallina californica* grazing on barnacle abundances ($\bar{x} \pm 1$ SD; 100 cm^2 areas) through time. The dashed line represents breakdown of the experimental fences.

1986	Experiment (-chitons)	Control (+chitons)
April 30	START	
May 13	0	0
July 23	1.3 ± 1.5	62.5 ± 47.4
September 6	0	48.3 ± 43.2
November 14	14.0 ± 19.8	55.5 ± 34.6

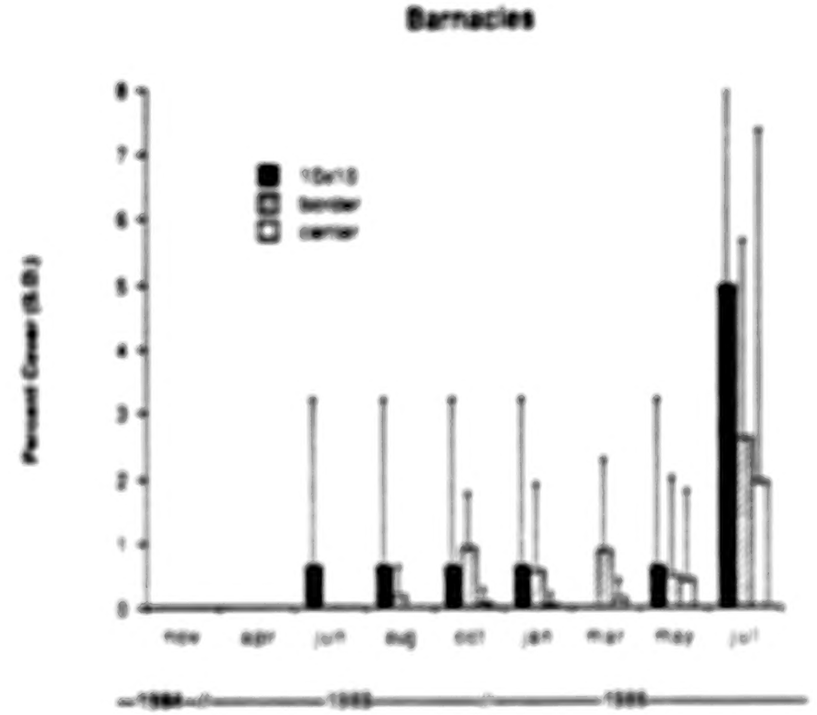


Figure 1-A-9a. Percent cover (± 1 SD; n = 4 for 10 x 10 plots, n = 12 for lumped borders and centers of other plot sizes) through time of barnacles (*Balanus* and *Chthamalus* combined).

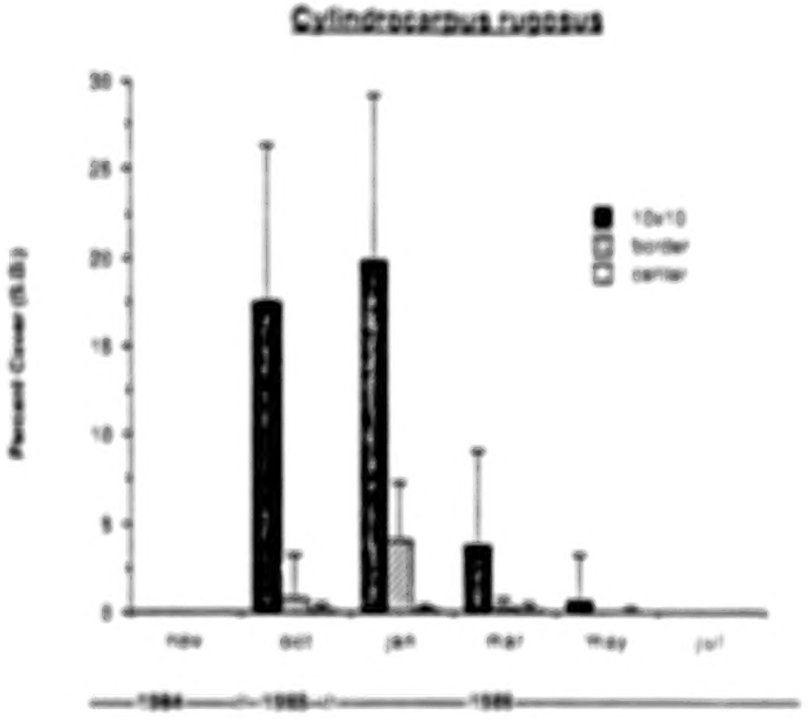


Figure 1-A-9b. Percent cover (± 1 SD; n = 4 for 10 x 10 plots, n = 12 for lumped borders and centers of other plot sizes) through time of *Cylindrocarpus rugosus*.

DISCUSSION

Partial Versus Complete Disturbances

In terms of comparative successional processes, the results of this study demonstrate a reduction of early successional species (*Ulva* sp(p); *Porphyra perforata*), complete inhibition of mid-successional species (*Iridaea flaccida*, *Egregia menziesii*), and a lack of edge effects in partially disturbed treatments compared to complete disturbances. The inhibition by algae of other species recruitment is common in marine intertidal systems (Dayton, 1975; Lubchenco and Menge, 1978; Sousa, 1979; Lubchenco, 1980; Foster, 1982; DeWreede, 1983; Foster *et al.*, 1988), with the notable exception of *Phyllospadix* sp(p)., an angiosperm, with barbed seeds that attach to earlier successional species (Dawson, 1966; Turner, 1983). Though some inhibiting algal species are foliose ephemerals, there is a definite advantage to the crustose base with upright frond morphology (e.g., *Bossiella plumosa*) in areas where partial disturbances are common. The basal portion can withstand the disturbance and inhibit recruitment of other species while regrowing upright fronds. Morphological adaptations such as this are more often associated with grazing (Lubchenco and Cubit, 1980; Dethier, 1981; Gaines and Lubchenco, 1982) and not physical disturbance regimes. The community result is that succession will differ with the level of disturbance severity.

The generalization proposed by Connell and Slatyer (1977), that less severe disturbances will recover more rapidly, seems to be holding true for this study. Although the study ended before the experimental plots were very similar to the controls, observations indicated that partially disturbed plots were more similar to the controls than were their completely disturbed counterparts. The late successional species, *Bossiella plumosa*, was more abundant and intermediate succession species were not present. Of course, factors such as tidal height (Suchanek, 1985; Underwood and Jernakoff, 1984) and wave exposure (Dayton, 1971, 1975; Menge, 1976; Underwood and Jernakoff, 1984) also affect recovery rates.

Our results suggest that dormant propagules are less important to subsequent succession in this mussel community than, for instance, in terrestrial fire communities (Christensen, 1985). Although the influence of propagules, analogous to seed banks in terrestrial communities (Kivilann and Bandurski, 1973; Harper, 1977; Westman, 1979), has not previously been tested in marine systems (Sousa, 1985), the unburned plots would have retained viable algal spores, but a bloom of species was not found.

Effects of Patch Size and Position Within Patch

The effects of patch size in mussel bed succession has been associated mostly with its effects on grazer abundances. Small patches have higher densities of grazers that affect algal species composition and abundance (Paine and Levin, 1981; Sousa 1984b; Suchanek, 1985). Sousa (1984b) tested the effects of grazing by creating two square patch sizes, 25 cm and 50 cm on a side, and eliminating limpets from some treatments with a copper paint barrier. He found that algal recruitment was indeed strongly affected by grazing. Small patches consisted of species which were resistant to grazers but were competitively inferior, while large patches contained species which were vulnerable to grazers but which were competitively superior.

One component of this study was the comparison of borders and centers of patches, which may also address the question of how size of clearings and grazers affect succession. The high densities of grazers in small patches is associated with their proximity to the surrounding community, not an inherent selection of small cleared areas by grazers. It has been suggested that "browse zones" at the borders of patches are caused by grazers leaving the mussel matrix to feed on algae in the patch during high tide, then returning to the mussels for refuge from desiccation and predators at low tide (Suchanek, 1978; Paine and Levin, 1981; Sousa 1985). The grazers are not all returning to the surrounding matrix because they are being counted in borders at low tide, therefore an additional hypothesis is presented. Algae and substratum irregularities caused by barnacles have been suggested and demonstrated to inhibit molluscan grazer attachment (Underwood and Jernakoff, 1981; Jernakoff, 1983). It is possible that the grazers enter the borders of patches from outside because there is less competition for attachment space. They do not spread to the center because there is initially plenty of food and eventually too much algae to maintain a foothold. This hypothesis is supported by the fact that browse zones do not move in as the mussel matrix spreads into the patch (De Vogelaere, personal observation).

Two general patterns of grazer densities in clearings within mussel beds are: (1) there are more grazers in the borders (Suchanek, 1978; Paine and Levin, 1981; Sousa, 1984b), and (2) they decline in density through time (See Figure 18 in Sousa, 1984b). The decline in grazer densities may be due to competition with thick algal mats for attachment space. This has been suggested as a mechanism for grazer decline in mussel beds by Sousa (1984b) and determined to be a factor eliminating limpets from low intertidal algal communities (Underwood and Jernakoff, 1981). Interestingly, *Nuttallina californica* in Stillwater Cove demonstrated the above grazer density patterns better than the limpets. Chiton densities were very high, possibly because they are well-suited to live on the irregular conglomerate substratum. In contrast to the results at this site, chiton grazing has been considered relatively unimportant at other locations (Vesco, 1980; Dayton, 1975; Sousa, 1984b).

The effects of grazing on an organism's distribution and abundance are related to morphology, chemical composition, and secondary interactions involving competition. As discussed earlier, the algal morphology of a basal crust with upright fronds is considered advantageous in reducing grazer effects (Lubchenco and Cubit, 1980; Dethier, 1981; Gaines and Lubchenco, 1982; Littler and Littler, 1983); the uneaten basal portions are able to regenerate and persist. If a species is unpalatable because it contains chemicals such as phenolics (Geiselman and McConnell, 1981), has low caloric value (Paine and Vadas, 1969; Littler and Littler, 1980), or is composed of difficult-to-ingest chemicals such as calcium carbonate (Steneck, 1982), it will also be more resistant to grazing. The grazer resistant species will become more abundant when their more palatable competitors are eaten by grazers (Sousa, 1984b).

The spatial differences in abundance of the algal species in complete clearings in this study may be explained by their resistance to grazing. Diatoms and *Ulva* species are ephemeral and have no known method to deter grazing. Their abundances were greatly reduced in the borders of patches. The species that showed no edge effects were *Iridaea flaccida*, which has a thick perennial basal crust (Hansen and Doyle, 1976; Hansen, 1977; Foster, 1982), *Egregia menziesii*, which contains phenolic compounds (Steinberg, 1985) and has a very thick, tough holdfast (Black, 1974), and *Bossiella plumosa*, a species with high calcium carbonate content and a basal crust (Abbott and Hollenberg, 1976). *Cylindrocarpus rugosus* is an annual brown algal crust (Abbott and Hollenberg, 1976; Dawson and Foster, 1982) that comes and goes, seemingly taking advantage of bare space provided by grazing. Our results (Table I-A-7 and Figure I-A-8) suppon the suggestions of Magre (1978) and Sousa (1979) that the removal of algal turf by grazers may reduce competition for space between barnacles and algae, and increase barnacle abundances. Conversely, it has been suggested that limpets may reduce barnacle cover at other sites by bulldozing (Dayton, 1971, Menge, 1976) or through feeding activity (Connell, 1961; Dayton, 1971). It may be that at this site barnacles are enhanced because of different radula effects, and the soft girdle of *Nuttallina* may be less abrasive than a scraping limpet shell.

When the effect of browse zones was factored out by subsampling, size of clearing was not found to affect colonization in the range considered. There were no significant differences in succession trends when comparing the centers of the three larger clearing sizes. The smallest patch size was very different from the larger ones, but this can be attributed to the browse zone extending over its whole area. The extended size range in this experiment reinforces Sousa's (1984b) conclusions for patch sizes in a mussel bed 225 kilometers to the north; where grazers are not eliminated, there is no correlation between recruitment and percent cover of conspecifics within one meter of a plot. Sousa (1984b), focusing on spore dispersal limitations, did suggest that recruitment would be related to local adult populations in large size patches where grazers do not reach the center. In this study, the largest size patches did not show this pattern, possibly because the distance to the centers of the plots was still short and the surrounding community around all plots seemed fairly uniform. More research is necessary on algal spore dispersal patterns.

General Perspectives

Patch dynamics are important in determining the structure of many communities, but the communities differ in the relative importance of their patch attributes. In communities dominated by species with rapid vegetative growth (e.g., sheet-like sponges: Ayling, 1983; subtidal colonial species: Keough, 1984), whether a patch is isolated or contiguous with the community is important. The species with rapid vegetative growth will quickly outcompete other species which will only succeed in isolated patches (Kay and Keough, 1981; Keough, 1984; Sousa, 1985; Connell and Keough, 1985). Patch edge effects may be caused by whiplash (Dayton, 1971; Grant, 1977), filter feeding (Young and Chia, 1987) by surrounding organisms, by changes in water motion (Foster, 1975), differential rodent grazing (Rice, 1987), and shading, nutrient, and water levels (Runkle, 1985).

Runkle (1985) suggests that different rates of disturbance select for different growth strategies. This study indicates that different disturbance severity regimes may also select for different intertidal plant morphologies. When the disturbance regime consists primarily of partial disturbances, algae with upright portions regenerating from crustose holdfasts will be more common than faster growing solitary species. An analogy can be drawn with the seeding versus resprouting strategies in fire communities under different severity regimes (Christensen, 1985).

Experimental clearings are widely used in marine ecology to study life histories, demography, competitive interactions, grazer effects, succession, and the mechanisms affecting many other distribution patterns (Foster and Sousa, 1985). Some of the rationale given for the use of small clearings is to avoid spore dispersal limitations, to ensure effective removal, or to use a convenient size without increasing statistical variability. Large clearings have been used to avoid edge effects, but the reason for using a particular clearing size is often not given (De Vogelaere, in prep.). Complete clearings are made to ensure similarity between replicates and to ensure spore removal, while partial clearings have been used to mimic a particular type of disturbance. This study has shown that size may not be important if it is larger than a minimal browse-zone distance (variable from one site to the next) or if grazers are excluded, and that there are different successional patterns depending on the severity of the clearing. Of course if the objective is to study the effects of a natural disturbance, the best method is to simulate natural clearing patterns found at a study site (Foster and Sousa, 1985). If this is not possible, then consideration of the above factors of disturbance size and severity are necessary.

REFERENCES

Abbott, I.A. and G.J. Hollenberg. 1976. Marine algae of California. Stanford University Press, Stanford, California.

Andrew, N.L. and B.D. Mapstone. 1987. Sampling and the description of spatial pattern in marine ecology. Oceanography and Marine Biology Annual Review 39.

Ayling, A.L. 1983. Factors affecting the spatial distributions of thinly encrusting sponges from temperate waters. Oecologia 60:412-418.

Barnes, H. and H.T. Powell. 1950. The development, general morphology and subsequent elimination of barnacle populations, *Balanus crenatus* and *B. balanoides*, after a heavy initial settlement. The Journal of Animal Ecology 19: 175-180.

Bertness, M.D. and A.M. Ellison. 1987. Determinants of pattern in a New England salt marsh plant community. Ecological Monographs 57:129-147.

Black, R. 1974. Some biological interactions affecting intertidal populations of the kelp *Egregia laevigata*. Marine Biology 28:189-198.

Boal, J. 1980. Pacific harbor seal (*Phoca vitulina richardii*) haul out impact on the rocky midtidal zone. Marine Ecology - Progress Series 2:265-269.

Bormann, F.H. and G.E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, Berlin, New York.

Christensen, N.L. 1985. Shrubland fire regimes and their evolutionary consequences. Pages 86-100 in S.T.A. Pickett and P.S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, London.

Connell, J.H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecological Monographs 31:61-104.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Connell, J.H. 1985. Variation and persistence of rocky shore populations. Pages 57-69 in P.G. Moore and R. Seed, editors. The ecology of rocky coasts. Hodder and Stoughton, London, Toronto.

Connell, J.H. and M.J. Keough. 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. Pages 125-151 in S.T.A. Pickett and P.S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, London.

Connell, J.H. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist 111:1119-1144.

Connell, J.H. and W.P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. The American Naturalist 121:789-824.

Connor, V.M. and J.F. Quinn. 1984. Stimulation of food species growth by limpet mucus. Science 225:843-844.

Cross, T.F. and T. Southgate. 1983. An approach to ecological monitoring in the rocky intertidal: a survey of Bantry Bay and Dunmanus Bay, Ireland. Marine Environmental Research 8:148-163.

Dawson, E.Y. 1966. Marine botany, an introduction. Holt, Rinehart and Winston, Inc., New York, San Francisco.

Dawson E.Y. and M.S. Foster. 1982. Seashore plants of California. University of California Press, Berkeley, London.

Dayton, P.K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41:351-389.

Dayton, P.K. 1973. Dispersion, dispersal, and persistence of the annual intertidal alga, *Postelsia palmaeformis* Ruprecht. Ecology 54:433-438.

Dayton, P.K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecological Monographs 45:137-159.

Denslow, J.S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. Oecologia 46:18-21.

Dethier, M.N. 1981. Heteromorphic algal life histories: the seasonal pattern and response to herbivory of the brown crust, *Ralfsia californica*. Oecologia 49:333-339.

Dethier, M.N. 1984. Disturbance and recovery in intertidal pools: maintenance of mosaic patterns. Ecological Monographs 54:99-118.

De Vogelaere, A. On the use of clearings in rocky intertidal field experiments. Manuscript in preparation.

De Wreede, R.E. 1983. *Sargassum muticum* (Fucales, Phaeophyta): regrowth and interaction and *Rhodomela larix* (Ceramiales, Rhodophyta). Phycologia 22:153-160.

Doty, M.S. 1967. Contrast between the pioneer populating process on land and shore. Bulletin of the Southern California Academy of Sciences 66:175-194.

Foster, M.S. 1975. Regulation of algal community development in a *Macrocystis pyrifera* forest. Marine Biology 32:331-342.

Foster, M.S. 1982. Factors controlling the intertidal zonation of *Iridaea flaccida* (Rhodophyta). Journal of Phycology 18:285-294.

Foster, M.S. and W.P. Sousa. 1985. Succession. Pages 269-290 in M.M. Littler and D.S. Littler, editors. Handbook of phycological methods. Cambridge University Press.

Foster, M.S., A.P. De Vogelaere, C. Harrold, J.S. Pearse, and A.B. Thum. 1988. Causes of spatial and temporal patterns in rocky intertidal communities of central and northern California. Memoirs of the California Academy of Sciences. No. 9. 45 pp.

Gaines, S.D. and J. Lubchenco. 1982. A unified approach to marine plant-herbivore interactions. 2. Biogeography. Annual Review of Ecology and Systematics 13:111-138.

Garwood, N.C., D.P. Janos and N. Brokaw. 1979. Earthquake caused landslides: a major disturbance to tropical forest. Science 205:997-999.

Geiselman, J.A. and O.J. McConnell. 1981. Polyphenols in brown algae *Fucus vesiculosus* and *Ascophyllum nodosum*: chemical defenses against the marine herbivorous snail, *Littorina littorea*. Journal of Chemical Ecology 7:1115-1133.

Grant, W.S. 1977. High intertidal community organization on a rocky headland in Maine, USA. Marine Biology 44:15-25.

Green, L.R. 1982. Prescribed burning in the California Mediterranean ecosystem. Pages 464-471 in C.E. Conrad and W.C. Oechel, editors. Dynamics and management of Mediterranean-type ecosystems. Pacific Southwest Forest and Range Experiment Station. General Technical Reports. PSW-58.

Hansen, J.E. 1977. Ecology and natural history of *Iridaea cordata* (Gigartinales, Rhodophyta) growth. Journal of Phycology 13:395-402.

Hansen, J.E. and W.T. Doyle. 1976. Ecology and natural history of *Iridaea cordata* (Rhodophyta; Gigartinaceae): Population structure. Journal of Phycology 12:273-278.

Harper, J.L. 1977. Population biology of plants. Academic Press, London, New York, San Francisco.

Holling, C.S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1-23.

Jernakoff, P. 1983. Factors affecting the recruitment of algae in a midshore region dominated by barnacles. Journal of Experimental Marine Biology and Ecology 67:17-31.

Kay, A.M. and M.J. Keough. 1981. Occupation of patches in the epifaunal communities on pier pilings and the bivalve *Pinna bicolor* at Edithburgh, South Australia. Oecologia 48:123-130.

Keough, M.J. 1984. Effects of patch size on the abundance of sessile marine invertebrates. Ecology 65:423-437.

Kinnetic Laboratories, Inc. 1986. Study of the rocky intertidal communities of central and northern California, Year I. Prepared in association with the University of California, Santa Cruz, Moss Landing Marine Laboratories, and TERA Corporation for the Pacific OCS Region, Minerals Management Service, U.S. Dept. of the Interior. Contract No. 14-12-0001-30057. OCS Study, MMS 86-0051. 448 pp.

Kivilaan, A. and R.S. Bandurski. 1973. The ninety-year period of Dr. Beal's seed viability experiment. American Journal of Botany 60:140-145.

Littler, M.M. and D.S. Littler. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory test of a functional form model. The American Naturalist 116:25-44.

Littler, M.M. and D.S. Littler. 1983. Heteromorphic life-history strategies in the brown alga *Scytosiphon lomentaria* (Lyngb.) Link. Journal of Phycology 19:425-431.

Lubchenco, J. 1980. Algal zonation in the New England rocky intertidal community: An experimental analysis. Ecology 61:333-344.

Lubchenco, J. and J. Cubit. 1980. Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. Ecology 61:676-687.

Lubchenco, J. and B.A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. Ecological Monographs 59:67-94.

Magre, E.J. 1974. *Ulva lactuca* L. negatively affects *Balanus balanoides* (L.) (*Cirripedia thoracica*) in tidepools. Crustaceana 27: 231-234.

Menge, B.A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecological Monographs 46:355-393.

Morris, R.H., D.P. Abbott, and E.C. Haderlie. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, California.

Northcraft, R.D. 1948. Marine algal colonization on the Monterey Peninsula, California. American Journal of Botany 35:396-404.

O'Clair, C.E. 1981. Disturbance and diversity in a boreal marine community: the role of intertidal scouring by sea ice. Pages 1105-1136 in D.W. Hood and J.A. Calder, editors. The eastern Bering Sea shelf: oceanography and resources. Volume 2. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of Marine Pollution Assessment. Distributed by the University of Washington Press.

Oliver, J.S. and P.N. Slattery. 1985. Destruction and opportunity of the sea floor: effects of gray whale feeding. Ecology 66:1965-1975.

Paine, R.T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93-120.

Paine, R.T. and S.A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs 51:145-178.

Paine, R.T. and R.L. Vadas. 1969. Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. Marine Biology 4:79-86.

Pickett, S.T.A. and P.S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York, London.

Rice, K.J. 1987. Interaction of disturbance patch size and herbivory in Erodium colonization. Ecology 68:1113-1115.

Ricketts, E.F., J. Calvin and J.W. Hedgpeth. 1985. Between Pacific tides. Stanford University Press, Palo Alto, California.

Runkle, J.R. 1985. Disturbance regimes in temperate forest. Pages 17-33 in S.T.A. Pickett and P.S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, London.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. Second edition. W.H. Freeman and Company, San Francisco.

Sousa, W.P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecological Monographs 49:227-254.

Sousa, W.P. 1980. The responses of a community to disturbance: the importance of successional age and species' life histories. Oecologia 45:72-81.

Sousa, W.P. 1984a. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353-391.

Sousa, W.P. 1984b. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. Ecology 65:1918-1935.

Sousa, W.P. 1985. Disturbance and patch dynamics on rocky intertidal shores. Pages 101-124 in S.T.A. Pickett and P.S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, London.

Specht, R.L. 1981. Primary production in Mediterranean-climate ecosystems regenerating after fire. Pages 257-267 in F. di Castri, D.W. Goodall, and R.L. Specht, editors. Ecosystems of the world, Volume 11, Mediterranean-type shrublands. Elsevier, Amsterdam, New York.

Steinberg, P.D. 1985. Feeding preferences of *Tegula funebralis* and chemical defenses of marine brown algae. Ecological Monographs 55:333-349.

Steneck, R.S. 1982. A limpet-coralline alga association: adaptations and defenses between a selective herbivore and its prey. Ecology 63:507-522.

Suchanek, T.H. 1978. The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. Journal of Experimental Marine Biology and Ecology 31:105-120.

Suchanek, T.H. 1985. Mussels and their role in structuring rocky shore communities. Pages 70-96 in P.G. Moore and R. Seed, editors. The ecology of rocky coasts. Hodder and Stougiston, London.

Turner, T. 1983. Facilitation as a successional mechanism in a rocky intertidal community. The American Naturalist 121:729-738.

Underwood, A.J. 1980. The effects of grazing by gastropods and physical factors of the upper limits of distribution of intertidal macroalgae. Oecologia 46:210-213.

Underwood, A.J. and P. Jernakoff. 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. Oecologia 48:221-233.

Underwood, A.J. and P. Jernakoff. 1984. The effects of tidal height, wave-exposure, seasonality and rock-pools on grazing and the distribution of intertidal macroalgae in New South Wales. Journal of Experimental Marine Biology and Ecology 75:71-96.

VanBlaricom, G.R. 1987. Effects of foraging by sea otters on mussel-dominated intertidal communities. Pages 48-91 in G.R. VanBlaricom and J.A. Estes, editors. The community ecology of sea otters. Ecological studies, volume 65. Springer, Berlin, Heidelberg, New York.

Vesco, L. 1980. Interactions between the rocky intertidal chiton *Nuttallina fluxa* (Mollusca: Polyplacophora) and other macroorganisms in a coralline algal community at Whites Point, Los Angeles, California. Master's Thesis, California State University, Fullerton.

Westman, W.E. 1979. A potential role of coastal sage scrub understories in the recovery of chaparral after fire. Madrono 26:64-68.

White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. Botanical Review 45:229-299.

Whittaker, R.J. and S.A. Levin. 1977. The role of mosaic phenomena in natural communities. Theoretical Population Biology 12:117-139.

Wiens, J.A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics 7:81-120.

Winer, B.J. 1971. Statistical principles in experimental design. McGraw-Hill, New York, London.

Young, C.M. and F.S. Chia. 1987. Abundance and distribution of pelagic larvae as influenced by predation, behavior, and hydrographic factors. Pages 385-463 in A.C. Giese, J.S. Pearse, and V.B Pearse, editors. Reproduction of marine invertebrates. Volume 9: General concepts. Blackwell Scientific - Boxwood Press, Palo Alto.

Zedler, P.H., C.R. Gautier and G.S. McMaster. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chapparal and coastal shrub. Ecology 64:809-818.

APPENDICES
to
APPENDIX A

APPENDIX A-1

Analysis of variance model to test for effects of plot size, position within plot, and replicates nested within size.

Size	S1				S2					S3		
Replicate Plots:	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12
Position:												
Border	n=3	3	3	3	3	3	3	3	3	3	3	3
Center	n=3	3	3	3	3	3	3	3	3	3	3	3

	Source of Variation	d.f.	Estimated Mean Square	F Ratio
A	Size	2	$\sigma^2_e + cn\sigma^2_{B(A)} + bcn\sigma^2_A$	MSA/MS/BW.A
BW.A	Plot within Size	9	$\sigma^2_e + cn\sigma^2_{B(A)}$	MSBW.A/MSres
C	Position	1	$\sigma^2_e + n\sigma^2_{B(A)C} + abn\sigma^2_c$	MSC/MS(BW.A)C
AC	Size x Position	2	$\sigma^2_e + n\sigma^2_{B(A)C} + bn\sigma^2_{AC}$	MSAC/MS(BW.A)C
(BW.A)C	Plot within Size x Position	9	$\sigma^2_e + n\sigma^2_{B(A)C}$	MS(BW.A)C/MSres.
	Residual = within cell	48	σ^2_e	

APPENDIX A-2

Analysis of variance model to test for effects of disturbance severity, position within plot, and replicates nested within severity.

Severity	Complete				Partial			
Replicate Plots:	P1	P2	P3	P4	P5	P6	P7	P8
Position:								
Border	n=3	3	3	3	3	3	3	3
Center	n=3	3	3	3	3	3	3	3

	Source of Variation	d.f.	Estimated Mean Square	F Ratio
A	Severity	1	$\sigma^2_e + cn\sigma^2_{B(A)} + bcn\sigma^2_A$	MSA/MS/BW.A
BW.A	Plot within Severity	6	$\sigma^2_e + cn\sigma^2_{B(A)}$	MSBW.A/MSres
C	Position	1	$\sigma^2_e + n\sigma^2_{B(A)C} + abn\sigma^2_c$	MSC/MS(BW.A)C
AC	Severity x Position	1	$\sigma^2_e + n\sigma^2_{B(A)C} + bn\sigma^2_{AC}$	MSAC/MS(BW.A)C
(BW.A)C	Plot within Severity x Position	6	$\sigma^2_e + n\sigma^2_{B(A)C}$	MS(BW.A)C/MSres.
	Residual = within Cell	32	σ^2_e	

APPENDIX B

Data Analysis and Equations

APPENDIX B

Data Analysis and Equations

TABLE OF CONTENTS

Page

Bray-Curtis Percent Similarity I-101

Dominance Function I-101

Shannon-Wiener Diversity I-101

Evenness I-102

Bray-Curtis Percent Similarity (Boesch, 1977; Goodall, 1978a,b; Pielou, 1984)

The Bray-Curtis percent similarity measure, also known as percent similarity or Czekanowski's index of similarity, is a quantitative resemblance measure. It is calculated by the expression:

$$PS = 200 \times \frac{\sum_{i=1}^{s} \min(x_{i1}, x_{i2})}{\sum_{i=1}^{s} (x_{i1} + x_{i2})}$$

where: s = number of species found in one or both quadrats

x_{i1} and x_{i2} = amount of species i in quadrats 1 and 2, respectively
i = 1, 2 ...... , s species.

Dominance Function, c (Whittaker, 1965; Washington, 1984)

This measurement of diversity is based on a quantitative relationship among species. The function c is a measurement of concentration of dominance as expressed by:

$$c = \Sigma(y/N)^2$$

where y is the "importance" of a given species (number of individuals, biomass, percent cover) and N is the sum of the "importance values" for all species in the sample.

Shannon-Wiener Diversity Measure, H' (Shannon and Weaver, 1949; Green, 1979)

This is the Shannon and Weaver measure of the information content per symbol of a code which uses S kinds of discrete symbols with probability of occurrence P_j. Any base logarithms can be used; we used base E.

It is calculated by the expression:

$$H' = -\sum_{j} P_j \log P_j$$

where P_j is the proportion of the population that is of the jth species.

Evenness, J' (Pielou, 1966a, 1966b, 1975; Washington, 1984)

This index estimates the evenness of abundances among species. Evenness ranges from near zero for samples in which the abundances of different species are very dissimilar, to one for samples in which all species have the same abundance.

This index was calculated by the expression:

$$J' = \frac{H'}{H'_{max}}$$

where H' is Shannon-Wiener Diversity, and H'_{max} is the natural logarithm of the total number of species present in the sample.

REFERENCES

Boesch, D.F. 1977. Application of numerical classification in ecological investigations of water pollution. Virginia Institute of Marine Science, Gloucester Point, VA. Environmental Research Laboratory, Office of Research and Development, U.S. Environmental Protection Agency. EPB-600/3-77-033. March. 114 pp.

Goodall, D.W. 1978a. Sample similarity and species correlation. *In*: R.H. Whittaker, Ed., Ordination of plant communities. W. Junk, The Hague, pp. 99-149.

Goodall, D.W. 1978b. Numerical classification. *In*: R.H. Whittaker, Ed., Classification of plant communities. W. Junk, The Hague, pp. 249-288.

Green, R.H. 1979. Sampling design and statistical methods for environmental biologists. A Wiley-Interscience Publication, John Wiley and Sons, New York. 257 pp.

Pielou, E.C. 1966a. Species-diversity and pattern diversity in the study of ecological succession. Journal of Theoretical Biology 13:131-144.

Pielou, E.C. 1966b. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 10:370-383.

Pielou, E.C. 1975. Ecological Diversity. John Wiley and Sons, New York. 165 pp.

Pielou, E.C. 1984. The interpretation of ecological data: a primer on classification and ordination. John Wiley & Sons, New York. 263 pp.

Shannon, C.H. and W. Weaver. 1949. The mathematical theory of communication. University of Illinois Press. 127 pp.

Washington, H.G. 1984. Review: Diversity, biotic and similarity indices. Water Res. 18:653-694.

Whittaker, R.H. 1965. Dominance and diversity in land plant communities. Science 147:250-260.

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the wisest use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to assure that their development is in the best interest of all our people. The Department also has a major responsibility for American Indian reservation communities and for people who live in Island Territories under U.S. Administration.

END

06/15/90